

# INVERTEBRATE ZOOLOGY

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## PREFACE

At the request of the publishers, the writer last year began a revision of his *Introduction to Zoology*, which appeared in 1912 and had never been revised. This book was originally limited to a few invertebrate animals which were described in considerable detail. By the addition of other types and a more extensive review of the principal groups of invertebrates the *Introduction to Zoology* developed into an *Invertebrate Zoology*. Teachers who wish to introduce college students to zoology by means of the study of a few types of invertebrates will find the revised text at least as useful as the original, although careful selection will be found necessary. However, the book in its present form is intended primarily for students who have completed a college course in General Biology or Introductory Zoology and wish to obtain a more comprehensive knowledge of invertebrate animals.

Invertebrate Zoology is the logical second course in zoology. In such a course a careful study is made of at least one type, and usually several types, belonging to each large phylum. These types are compared with other members of the phylum and as large a number of common species are examined as time and opportunity afford. As usual the phyla are arranged according to their supposed position in the evolutionary series. Every group of invertebrates is included except those that belong in the phylum Chordata. These are ordinarily studied in courses in Vertebrate Zoology and hence are omitted here. The writer has made an earnest effort to bring the book up to date by the inclusion of the results of recent investigations. It should be realized, however, that many gaps exist in our knowledge of even the commonest of invertebrates, and that many facts and theories of a controversial nature make it impossible to give a complete account of any species or group. In every case of doubt what appeared to be a reasonable account is presented.

Many illustrations new to text books, some never before published, have been used to supplement the descriptions. Often a figure is more valuable than several pages of text in presenting the structure and physiological processes of an animal. Attention is



directed particularly to the eight full page plates which have been so well executed by Barbara Bradley Root. All illustrations that have been copied from other books or original publications are acknowledged in the legends. Many of them have been modified so as to bring out more distinctly the topography of the various systems of organs; of these a considerable number have been obtained from the recent book on *Invertebrata* by Borradaile and Potts.

It is desirable that students consult original sources and no doubt many who become especially interested in certain animals, structures, or principles will wish to obtain more information than it was possible to include here. On this account the following list of general reference books is included and a short, selected list of books and articles is added at the end of each chapter.

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BALTIMORE, MARYLAND

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# INVERTEBRATE ZOOLOGY

## CHAPTER I

### PHYLUM PROTOZOA

#### INTRODUCTION

PROTOZOA are the simplest of all animals and constitute the first or lowest phylum in the animal series. They are mostly microscopic in size and, hence, are not ordinarily seen except with the aid of a microscope. However, when millions of them are congregated together they form conspicuous masses; for example, flagellates of the genus *Euglena* may be so numerous at the surface of a fresh-water pond as to color the water green, and other types of protozoa that may be cultivated in glass dishes in the laboratory may be so numerous as to give a cloudy appearance to the culture medium. Single individuals of some of the larger protozoa, such as the ciliate *Paramecium*, can be seen with the naked eye if the proper background is provided.

Two types of protozoa exist with respect to their habitats. One type live in fresh water, salt water, or in moist places and are known as free-living protozoa. The other type live in or upon the bodies of other animals or plants and are called parasitic protozoa. One environmental condition is necessary for both types and that is the presence of sufficient moisture to prevent drying. Only the resistance spores or cysts of certain species of protozoa are able to withstand dessication.

Free-living protozoa are not distributed among bodies of water in a haphazard fashion but each species is more or less restricted to a definite type of habitat just as are higher animals. Some species live in fresh water; others, only in salt water; some live in contact with the bottom; others, float about suspended in the water; some are known to live only in the soil, and others, only in sphagnum swamps. Free-living protozoa are to be found almost everywhere on the surface of the earth where moisture exists.



Parasitic protozoa are likewise rather definitely restricted in their habitats. Every higher animal that has been carefully studied has been found to harbor parasitic protozoa. Each species of animal, as a rule, is parasitized by its own peculiar species of protozoa. For example, twenty-five different species of protozoa are known to live in man. Most of these species appear to occur in monkeys also, but only a few of them have been recorded from other animals. The parasitic species are usually separated into two groups; those that live in the digestive tract are known as intestinal protozoa and those that live principally in the blood, as blood-inhabiting protozoa.

The number of species of protozoa is very great and can hardly be estimated. Thousands of species of free-living protozoa have been described, and each species of higher animal seems to possess one or more species of protozoa peculiar to itself, hence the number of parasitic protozoa must be at least as great as that of all other animals combined. The number of individuals is likewise enormous. Billions of free-living species may exist in a single pond. Among parasitic species we need only refer to the millions of ciliates that occur in the stomach of cattle and the millions of flagellates that live in the cecum of almost every rat.

These immense numbers of protozoa are not difficult to separate into groups and ordinarily are placed in four classes according to the presence or absence of locomotor organs and the character of these when present. The four classes are as follows:

CLASS I. SARCODINA. Type: *Amæba*. Protozoa that move by means of pseudopodia (Fig. 1).

CLASS II. MASTIGOPHORA. Type: *Euglena*. Protozoa that move by means of flagella (Fig. 23).

CLASS III. SPOROZOA. Type: *Monocystis*. Protozoa without motile organs but with a spore stage in their life cycle (Fig. 40).

CLASS IV. INFUSORIA. Type: *Paramæcium*. Protozoa that move by means of cilia (Fig. 46).

## 1. CLASS I. SARCODINA

### (1) AMÆBA PROTEUS

*Amæba proteus* (Fig. 1) is a one-celled animal about .25 mm. ( $\frac{1}{100}$  inch) in diameter, and is, therefore, invisible to the naked eye. Under the compound microscope it appears as an irregular colorless

particle of animated jelly which is constantly changing its shape by thrusting out finger-like processes.

**Habitat.** — *Amæba proteus* lives in fresh-water ponds and streams. It may be obtained for laboratory use from a variety of places, such as the organic ooze from decaying vegetation or the lower surface of lily pads. About two weeks before the specimens are needed, a mass of pond weed (*Ceratophyllum* is the best) should

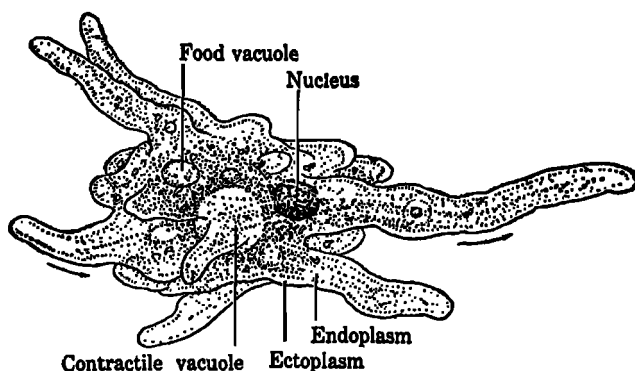


FIG. 1. — *Amæba proteus*. The arrows indicate the direction of streaming of the protoplasm. (From Woodruff.)

be gathered, placed in flat dishes, and immersed in water. The vegetation soon decays, and a brown scum appears on the surface. In this scum amœbæ may be found.

The fact that amœbæ appear in large numbers in cultures, such as just described, indicates that decaying pond weed furnishes a good habitat for them. Here they find their food, which consists of small aquatic plants, such as *Oscillaria* and diatoms, other protozoa, bacteria, and other animal and vegetable matter. While looking for an amœba note the character of its habitat.

**General morphology** (Fig. 1). — Two regions are distinguishable in the body of *amæba*, — an outer colorless layer of clear cytoplasm, the *ectosarc*, consisting of ectoplasm, and a comparatively large central mass of granular cytoplasm, the *endosarc*, consisting of endoplasm. A single clear spherical body, usually lying near the end of the animal away from the direction of motion, and disappearing at more or less regular intervals, is the *contractile vacuole*. Suspended in the endosarc is a *nucleus*, usually one or more *food vacuoles*, material ready for excretion. foreign substances such as

grains of sand, and undigested particles, the amount of the latter depending upon the feeding activity of the specimen at the time when examined.

From this description it will be noted that *Amæba proteus* contains all of the essential constituents of a cell. It is, moreover, simple in structure, shows a number of physiological activities in their simplest form, is one of the most primitive of all animals,

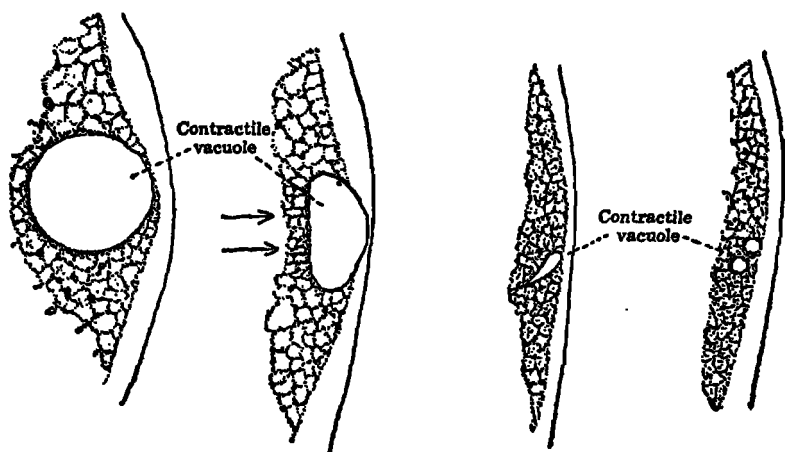


FIG. 2. — *Amæba proteus*. Four stages in the contraction of a contractile vacuole. (From Calkins.)

and is easily obtained. For these reasons it has been, and still is, a favorite animal for investigation.

**Cytology.** — The *ectoplasm* is easily distinguished from the endoplasm because of the absence within it of granules. It is firmer than the endoplasm.

The *endoplasm* occupies the central portion of the body. Being less dense than the ectoplasm, it contains within it all of the large granules. No fixed line of separation between it and the ectoplasm is visible.

The *nucleus* is not easily seen in living specimens. In animals that have been properly killed and stained it appears as a biconcave disk in young specimens but is often folded and convoluted in older specimens. Its position in the endoplasm is not definite, but changes during the movements of the amœba. It has a firm membrane and contains a great many spherical particles of chromatin scattered about in the nuclear sap. During the life of an amœba,

before the period of reproduction, the nucleus plays an important rôle in the metabolic activity of the cell. This has been proved by experiments in which the animal was cut in two. The streaming of the cytoplasm ceases within a few minutes in the piece without a nucleus but is resumed after a few hours. The enucleated amoeba may attach itself to the substratum and exhibits irritability although its responses to stimuli are modified. Food bodies are engulfed and digested in apparently a normal manner but death finally ensues. The part with the nucleus continues its life as a normal amoeba. Profound changes in the nucleus take place during reproduction; these will be described in detail later.

The *contractile vacuole* (Fig. 2) is a clear space filled with a fluid less dense than the surrounding protoplasm. It derives its name from the fact that at more or less regular intervals it suddenly disappears, its walls having contracted, thus forcing out the

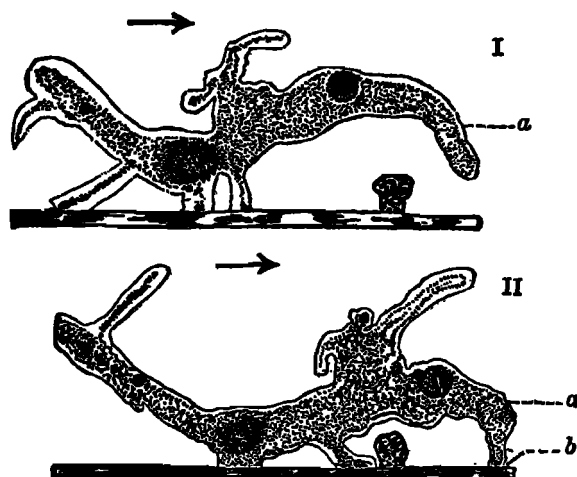


FIG. 3. — *Amoeba proteus*: locomotion. Two positions of an *Amoeba* advancing in the direction indicated by the arrows. I shows a pseudopod, *a*, being thrown over and beyond an inert object. In II pseudopod, *a*, has been fixed to substratum at *b*, and the body-proper has been dragged forward by the apparent contraction of *a*. (From Kepner, after Dellinger.)

contents. That the vacuole discharges to the outside of the body is difficult to prove in amoeba, no doubt because the fluid is usually expelled on the upper surface of the body and therefore cannot be seen. "At first the vacuole lies near the nucleus, but as it grows, it becomes separated from the latter, and at the time of its contraction lies at the end of the body farthest from the advancing pseudopodia, at what is sometimes called the posterior end. Its reappearance is always somewhere near its point of disappearance. While

still small it is carried along by the streaming protoplasm back to a position near the nucleus, where it completes its development."

The functions of the contractile vacuole are probably excretory and respiratory. It is also regarded as a hydrostatic organ, regulating the quantity of water contained in the body of the animal, and so, its weight. This would also afford a means of getting rid of the water taken in by the protoplasm through the body wall and consequently of regulating the tension between the protoplasm and the surrounding water. Death by diffuence is thus prevented.

*Food vacuoles* (Figs. 1, 4) are produced when food is taken into the body. Such a vacuole contains a particle of nutritive material and is a sort of temporary stomach.

**Physiology.** — Although extremely simple in structure, amoeba carries on practically all of the vital activities characteristic of the higher animals. It is capable of automatic movement, of reacting to various stimuli, of carrying on metabolic processes, of growth, and of reproduction. These are all fundamental properties of protoplasm and are here exhibited in their simplest form.

*Locomotion.* — Amœba moves from place to place by means of finger-like protrusions of the body, known as *pseudopodia* (Figs. 1, 3). A pseudopodium is formed in the following manner. The ectoplasm is pushed out and enlarged until a blunt projection is produced; the endoplasm then flows into it. The result is a movement of the entire animal in the direction of the pseudopodium. If more than one are formed at the same time, one usually survives while the others flow back and gradually disappear. Amœba moves, therefore, by thrusting out pseudopodia and then flowing into them. Amœba thus possesses an axiate organization that is continually changing and in this respect differs from most other protozoa and higher animals which have a fixed organization.

Amœba no doubt consists of a complex series of colloidal substances, and recent investigations indicate that the formation of pseudopodia is probably concerned with such phenomena as solation and gelation.

According to the most recent work, the body of an amoeba is divided into four parts (Fig. 4): (1) the *plasmasol* which is a central elongated portion, (2) the *plasmagel* which is a solid layer surrounding the plasmasol, (3) the *plasmalemma* which is a very thin elastic surface layer or membrane, and (4) a *hyaline layer* between the plasmagel and the plasmalemma. The plasmasol and

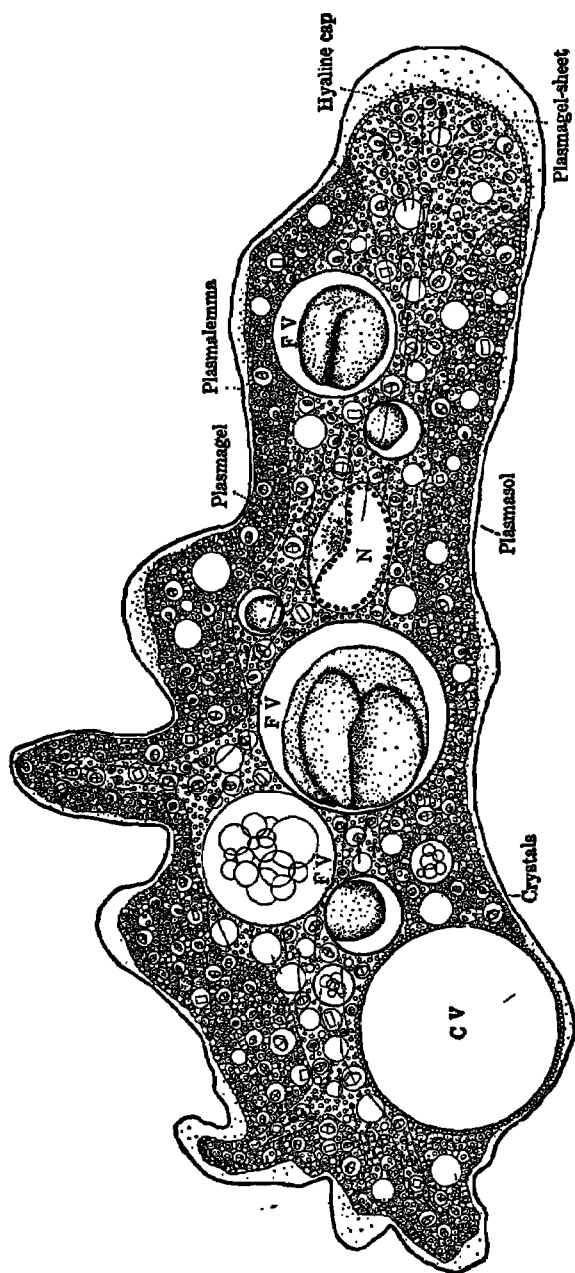


FIG. 4. — *Ameba proteus*: cytology. Horizontal optical section showing nucleus (N), contractile vacuole (CV), food vacuoles (FV). (After Mast.)

the plasmagel constitute the endoplasm, and the hyaline layer and the plasmalemma constitute the ectoplasm.

"There are four primary processes involved in locomotion in *Amæba*, attachment to the substratum, gelation of plasmasol at the anterior end, solation of the plasmagel at the posterior end and contraction of the plasmagel at the posterior end.

Ordinarily gelation of the plasmasol at the anterior end extends the plasmagel tube forward as rapidly as it is broken down at the posterior end by solation.

Contraction of the plasmagel tube at the posterior end drives the plasmasol forward.

The plasmagel tube is sometimes open at the anterior end and the plasmasol extends forward and comes in contact with the plasmalemma at this end but at other times it is closed by a thin sheet of gel which prevents the plasmasol from reaching the anterior end. This gel sheet at times persists intact for considerable periods, being built up by gelation as rapidly as it is broken down by stretching, owing to the pressure of the plasmasol against it. Usually it breaks periodically at various places. Sometimes the breaks are small and only a few granules of plasmasol pass through and these gelate immediately and close the openings. At other times the breaks are large and the plasmasol streams through filling the hyaline cap, after which the sol adjoining the plasmalemma gelates forming a new gel sheet.

An amœba is a turgid system, owing to this the plasmagel is continuously under tension. The plasmagel is elastic and consequently is pushed out at the region where its elastic strength is lowest. This results in the formation of pseudopods.

If an amœba is in an elongated form and is traveling, the elastic strength of the plasmagel is highest at the sides, lowest at the anterior end, and intermediate at the posterior end. This results in the production of the elongated form and in extension of the anterior end, after this form is produced.

If pressure is brought to bear against the anterior end the direction of flow of the plasmasol is immediately reversed, a new hyaline cap is formed at the posterior end which is thus transformed into a new anterior end. If pressure is directed against one side of the anterior end the direction of extension is deflected toward the opposite side." (Mast.)

Locomotion in the shelled rhizopod, *Diffugia* (Fig. 5), is in-

teresting when compared with that of *Amœba*. The pseudopodia are extended through the opening of the shell one after another and attached to the substratum at the tip. The pseudopodium then contracts and the shell containing the body is drawn forward. Successive extensions and contractions of pseudopodia result in intermittent locomotion. The details of the movements of *Diffugia* are as follows.

"The elastic strength of the plasmagel is lowest at the tip of the pseudopods. This results in contraction of the plasmagel elsewhere, and this contraction forces the plasmasol out through the plasmagel tube, causing expansion at the tip of the pseudopod.

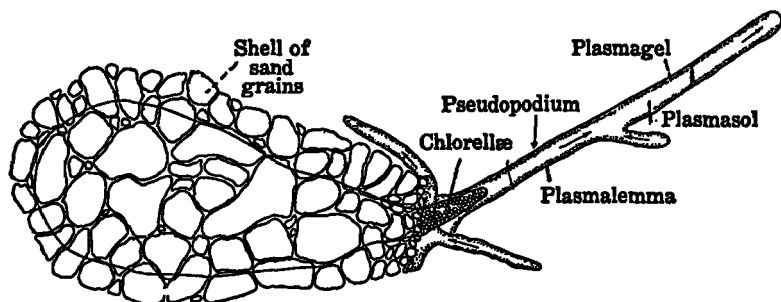


FIG. 5. — *Diffugia pyriformis* in locomotion. The arrows show the direction of the currents in the plasmasol. The plasmagel is indicated by dots. The protoplasm within the shell, indicated by the solid line, contained many chlorellæ. (After Mast.)

The plasmasol which is in contact with the distal edge of the plasmagel tube continuously gelates and this results in extension of the tube.

After the tip of the pseudopod becomes attached, the plasmasol in the tip gelates and the plasmagel throughout the entire pseudopod thickens greatly owing to gelation of adjoining plasmasol. This increases the elastic strength of the plasmagel in the entire pseudopod until it becomes greater here than elsewhere, after which it contracts and the pseudopod becomes shorter and thicker and the plasmasol in it is forced back into the body of the organism."

The contraction of the pseudopodia is much more pronounced in *Diffugia* than in *Amœba*. In the former, unequal local contraction of the plasmagel on opposite sides results in lateral movements of the pseudopodia. Contact stimuli on one side of a pseudo-



podium results in the thickening of the plasmagel in that region and a corresponding sharp bending movement. Such a stimulus may result in gelation at some distance from the region stimulated and hence "transmission of something akin to an impulse in higher forms" occurs. When the true explanation of amoeboid movement is found, it will probably give a key not only to the formation of pseudopodia but to the movement of flagella, cilia, and even muscular contraction. (Mast.)

*Metabolism.* — Growth in any living thing involves a complex series of changes. The chemical compounds which make up the bodies of animals are extremely labile; they are constantly breaking down into simpler substances or becoming more complex by the addition of new materials. There is no time during the life of any individual when elaborate chemical reactions are not taking place. *Metabolism* is the term used to include this great complex of incessant changes. Those processes which use energy to build up compounds are said to be *anabolic*; those which destroy substance to produce energy are termed *katabolic*.

Animals are primarily katabolic organisms. They cannot make organic compounds from simple inorganic substances; in this respect they differ from plants which manufacture starch from carbon dioxide and water. Since animals must have organic food, it follows that plant products are necessary either directly or in the form of protoplasm built up by other animals out of plant food. Before animal growth is possible, food must be converted into living substance. By the process of digestion food is prepared for absorption. Some substances that cannot be digested are passed out of the body as *fæces*. After absorption, food is carried to some part of the body where it is needed; here it is transformed into living substance by the process of *assimilation*.

In order that metabolic activity may go on without ceasing, a constant supply of energy is necessary. This energy is in part furnished by *oxidation*, *i.e.* the chemical union of oxygen with the living substance in a manner which may be compared to the changes taking place during combustion. *Respiration* supplies the oxygen for such metabolic activities, and also eliminates certain gaseous excretory products. The waste products formed by the breaking down of living substance are cast off as *excretions*. These should not be confused with *fæces*, which never have actually be-

come constituents of living matter. *Urea* is the most important of these excretory products.

In amoeba metabolic processes are seen in their simplest form. The entire series of processes connected with the manufacture and destruction of protoplasm are the ingestion of food, digestion, egestion, absorption, circulation, assimilation, dissimilation, secretion, excretion, and respiration.

*Food.* — The food of amoeba consists of very small aquatic plants such as *Oscillaria*, and diatoms, protozoa, bacteria, and other animal and vegetable matter. Animals that ingest solid food particles are said to be *holozoic*. A certain amount of choice of food is exercised, or the amoeba's body would become overloaded with particles of sand and other indigestible material among which it lives. Furthermore, amoeba seems to evince a preference for diatoms which one would think too large for easy consumption. This apparent *choice of food* may be due to ordinary physical laws of fluids.

*Ingestion.* — The ingestion, or taking in of food (Fig. 6), occurs without the aid of a mouth. Food may be engulfed at any point on the surface of the body, but is usually taken in at what may be called the temporary anterior end, that is, the part of the body toward the direction of locomotion. Jennings describes ingestion as follows. The amoeba flows against the food particle, which does not adhere but tends to be pushed forward away from the animal. That part of the body directly back of the food ceases its forward movements while, on either side and above, pseudopodia are extended which gradually form a concavity in which the food lies, and finally bend around the particle until their ends meet and fuse. A small amount of water is taken in with the food, so that there is formed a vacuole whose sides were formerly the outside of the body, and whose contents consist of a particle of nutritive material suspended in water. The whole process of food-taking occupies one or more minutes, depending on the character of the food. Amoeba is not always successful in accomplishing what it undertakes, but when it does not capture its prey at once, it seems to show a persistence usually only attributed to higher organisms. No doubt the reactions in food-taking depend upon both mechanical and chemical stimuli.

*Digestion.* — Digestion takes place without the aid of a stomach. After a *food vacuole* has become embedded in the endoplasm

its walls pour into it a secretion of some mineral acid, probably HCl. "It is probable that the minute particles of nucleoproteids that are constantly arising in the neighborhood of the nucleus contain certain digestive ferments which stimulate the formation

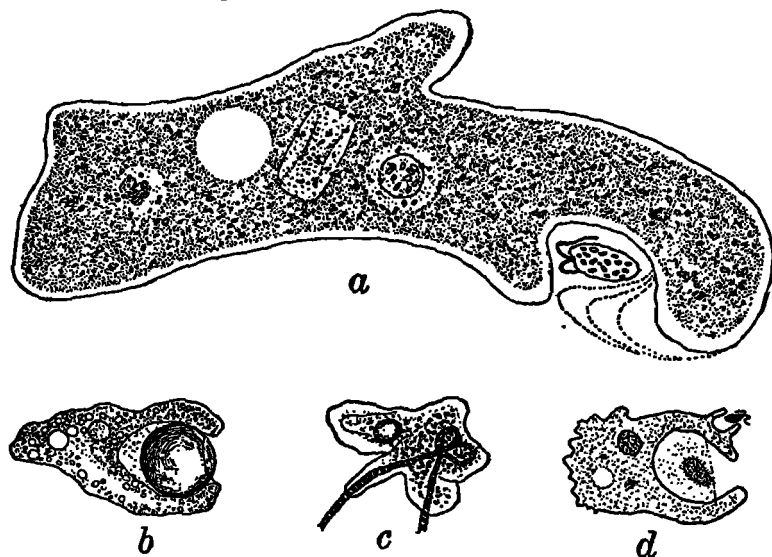


FIG. 6. — *Amœba*. Ingestion of food. a, Successive positions of a pseudopodium of an amoeba capturing a flagellate, *Chilomonas*. b, Ingesting a cyst of a flagellate, *Euglena*. c, Ingesting a filament of *Oscillaria*. d, A food cup for ingesting a flagellate superimposed on a food cup containing a ciliate. (a, after Kepner and Taliaferro; b, after Jennings; c, after Rhumbler; d, after Becker.)

of the mineral acid in the vicinity of the gastric vacuole." The digestive fluid dissolves protein substances, and perhaps also fats and sugars, but not starch.

*Egestion.* — Indigestible particles are egested at any point on the surface of the amoeba, there being no special opening to the exterior for this waste matter. Usually such particles are heavier than the protoplasm, and as the animal moves forward they lag behind, finally passing out at the end away from the direction of movement; that is, amoeba flows away, leaving the indigestible solids behind. This process is not so simple in such a species as *Amœba verrucosa* which possesses an ectoplasmic pellicle that is a thick, tough membrane. Waste pellets are extruded as shown in figure 7, a new pellicle being formed at the point of exit which prevents the outflow of the endoplasm.

**Assimilation.**—The peptones, derived from the digestion of protein substances, together with the water and mineral matter taken in when the gastric vacuole was formed, are absorbed by the surrounding protoplasm and pass into the body substance of the animal, no circulatory system being present so far as we know. These particles of organic and inorganic matter are then assimilated; that is, they are rearranged to form new particles of living protoplasm, which are deposited among the previously existing particles. The ability to thus manufacture protoplasm from unorganized matter, is one of the fundamental properties of living substance.

**Dissimilation.**—The energy for the work done by amœba comes from the breaking down of complex molecules by oxidation

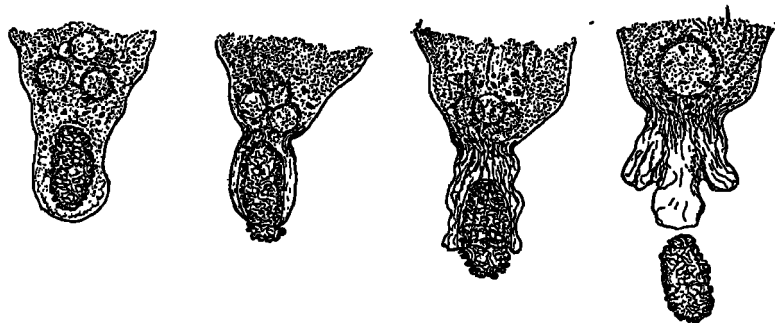


FIG. 7. — *Amœba verrucosa*. Four stages in the ejection of a waste pellet. Note the rigidity of the pellicle. (After Howland.)

or “physiological burning.” This is known as dissimilation or *katabolism*. The products of this slow combustion are the energy of movement, heat, and residual matter. Ordinarily the residual matter consists of solids and fluids, mainly water, some mineral substances, urea, and  $\text{CO}_2$ . Secretions, excretions, and the products of respiration are included in this list.

**Secretion.**—We have already noted that an acid is poured into the gastric vacuoles by the surrounding protoplasm. Such a product of dissimilation, which is of use in the economy of the animal, is known as a secretion.

**Excretion.**—Materials representing the final reduction of substances in the process of *katabolism* are called excretions. These are deposited either within or outside of the body. A large part of the excretory matter, including urea and  $\text{CO}_2$ , passes through

the general surface of the body. The fluid content of the contractile vacuole is known to contain urea, therefore this organ is excretory in function.

*Respiration.* — The contractile vacuole is also respiratory, since  $\text{CO}_2$  probably makes its way to the exterior by way of this organ.

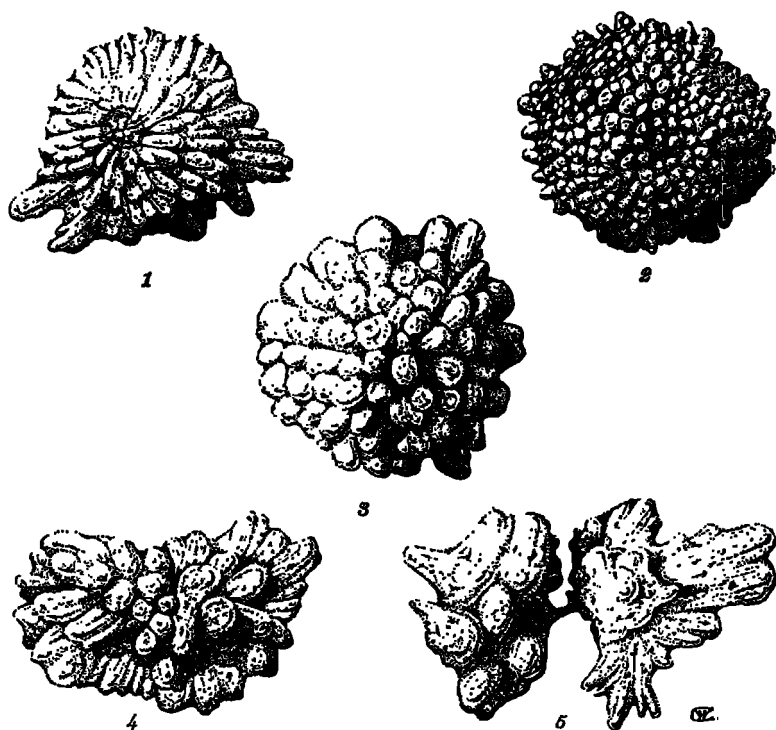


FIG. 8A. — *Amœba proteus*. Binary division. The external appearance of the organism at various stages during nuclear division. 1, just before the formation of the division sphere. 2, typical appearance during early stages of division. 3, just before elongation. 4, elongating stage. 5, division almost completed. (From Chalkley and Daniel.)

Oxygen dissolved in water is taken in through the surface of the body. This gas is necessary for the life of the animal; if replaced by hydrogen, movements cease after twenty-four hours; if air is then introduced, movements begin again; if not, death ensues.

*Growth.* — If food is plentiful, more substance is added to the living protoplasm of the amœba than is used up in its various physical activities. The result is an increase in the volume of the

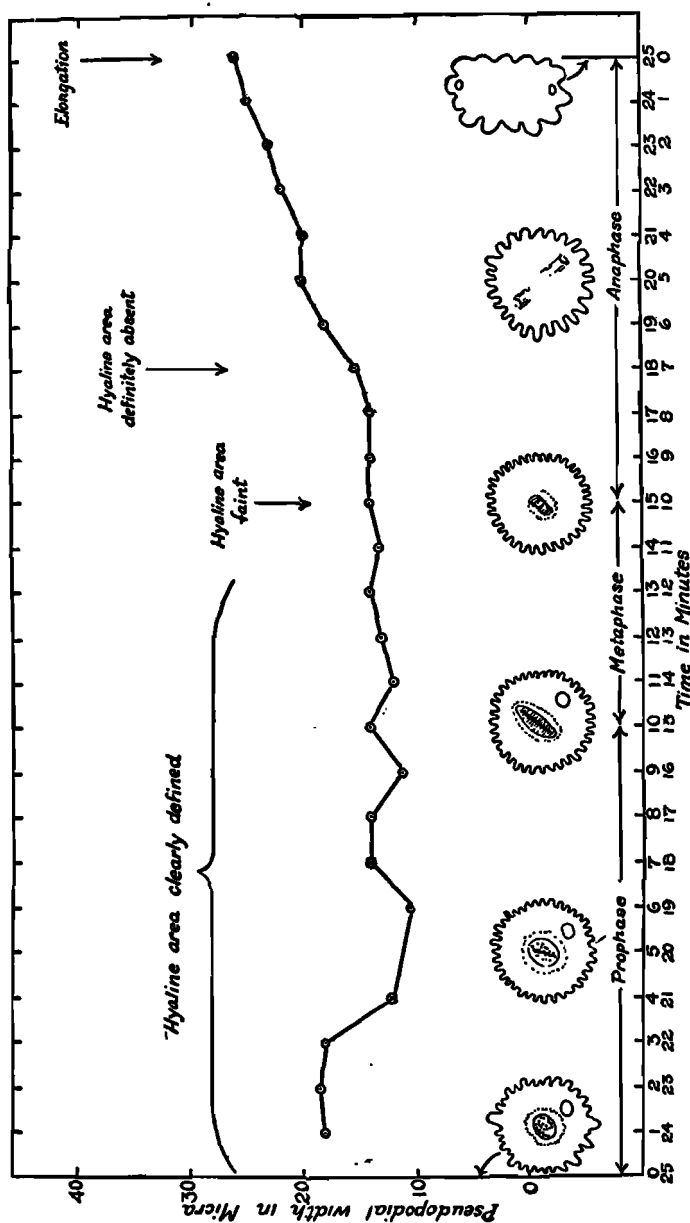


FIG. 8B. — Graph showing the nuclei of *Ameba proteus* during the prophase, metaphase and anaphase of mitosis; the time in minutes required for each stage; the duration of the hyaline area; and, by a curve, the width of the pseudopodia at various stages. (From Chalkey and Daniel.)

animal. This is growth, and, as in all other living organisms, growth by the addition of new particles among the preexisting particles, *i.e.* growth by *intussusception*.

*Reproduction* (Figs. 8A and 8B). — There is, however, a limit with regard to the size that may be attained by *Amæba proteus*, as it rarely exceeds .25 mm. ( $\frac{1}{100}$  inch) in diameter. When this limit is reached, the animal divides into two parts. It is supposed that this division is inaugurated through some unknown change in the relations between the nucleus and the cytoplasm.

There is only one type of reproduction in *Amæba proteus* of which we are certain; this is *binary division*. Sporulation and other types of reproduction have been described by investigators but have never been satisfactorily established. The most recent description of the binary division of *Amæba proteus* is as follows (Fig. 8A). "The nucleus divides *promitotically* and the nuclear membrane disappears at metaphase (Fig. 8B). The average time for the division process at a temperature of 24° C. is 33 minutes, with an average deviation of about 2 minutes. The *prophase* lasts about 10 minutes, the *metaphase* not over 5 minutes, probably less, the *anaphase* about 10 minutes, and the *telophase* about 8 minutes. The nuclear phases are accompanied by typical changes in cell form that are readily distinguishable under a magnification of 30 diameters. During prophase the cell is spherical, studded with fine pseudopodia and exhibits under reflected light a clearly defined hyaline area at its center (Fig. 8A). During metaphase the picture is similar, except that the hyaline area is very faint. During anaphase the pseudopodia become rapidly coarser, and the hyaline area is no longer visible. The telophase is accompanied by elongation of the cell and cleft formation.

Under the cultural conditions used, the average measured width of the pseudopodia in early prophase was 18 micra; from mid prophase to metaphase it was 13 to 14 micra. At anaphase the average width began to increase and at the beginning of telophase attained a value of 26 micra. It is possible merely from observation of the external appearance of the living cell to select from culture under a magnification as low as 30 diameters cells showing any desired stage of *nuclear* division except actual metaphase. Such selection can readily be made with 97 per cent accuracy, thus making possible the study of the effect of reagents upon the separate nuclear phases in cell division. The modal volume of *Amæba proteus* at

division under the cultural conditions employed is .0027 cubic millimeters. Binucleate forms are produced in culture by failure of cytoplasmic fission. Evidence is presented that the contractile vacuole ceases to function during division from the time that the nucleus enters the metaphase stage until cell division is completed. The close correlation of the disappearance of the nuclear membrane with the cessation of the activity of the contractile vacuole and the beginning of the rapid increase in average width of the pseudopodia during the nuclear anaphase, suggests a causative relation between these phenomena." (Chalkley and Daniel.)

The *development* of amoeba is simply a matter of growth; the daughter cells resulting from binary division become full-grown specimens by means of a gradual increase in volume.

**Behavior.** — The sum total of all the various movements of an animal constitute what is known as its behavior. In amoeba these movements may be separated into those connected with locomotion and those resulting from external stimuli. We have already given an account of the locomotion of amoeba, and so shall confine ourselves now to a discussion of its responses to different kinds of stimuli. The reactions of amoeba to stimuli have been grouped by Jennings into positive, negative, and food-taking. The last named were discussed on page 11. The following account, then, will deal with positive and negative reactions of *Amoeba proteus* to external stimulation.

**Reactions to stimuli.** — Amoebæ react to various kinds of stimuli including contact, chemicals, heat, light, and electricity.

If the animal reacts by a movement toward the stimulus, such as light, it is said to react *positively*; if away from the stimulus, *negatively*.

Amoeba reacts negatively when touched at any point with a solid

object; the part affected contracts and the animal moves away (Fig. 9). When, however, an amoeba is floating freely in the water and a pseudopodium comes in contact with the substratum, the animal moves in the direction of that pseudopodium until the

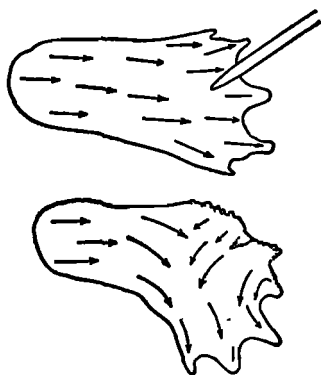


FIG. 9. — *Amoeba*: reaction to contact. A specimen moves away from a mechanical stimulus. (From Jennings.)



normal creeping position has been attained (Fig. 10). Contact with food also results in positive reactions. Amœba, therefore, reacts negatively to a strong mechanical stimulus and positively to a weak one.

Reactions to chemicals prove that amœba is sensitive to changes in the chemical composition of the water surrounding it. "It has

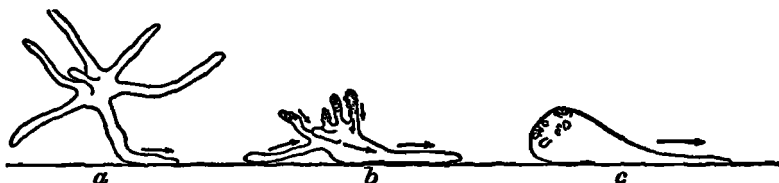


FIG. 10. — *Amœba*: reaction to contact. Changes in shape when a floating amœba encounters a solid. (From Jennings.)

been shown to react negatively when the following substances come in contact with one side of its body; methylene blue, methyl green (Fig. 11), sodium chloride, sodium carbonate, potassium nitrate, potassium hydroxide, acetic acid, hydrochloric acid, cane sugar, distilled water, tap water, and water from other cultures than that in which the amœba under experimentation lives." Experimental studies indicate that amœbæ are able to "sense" food some distance away; this is probably the result of chemical stimuli.



FIG. 11. — *Amœba*: reaction to a chemical. Methyl green results in a negative reaction. (From Jennings.)

Changes in the environment have a profound influence on the shape of amœba. When an organism is transferred from culture fluid to pure water it becomes radiate in form. If it is then placed in the proper concentration of any one of a number of salts it changes its form as indicated in figure 12. The form assumed by the organism appears to depend directly upon its water content.

Negative reactions result if amœba is locally affected by heat, since the animal will move away from heat stimuli. Cold and excessive heat retard its activities, which cease altogether between 30° and 35° C.

Amœba will orient itself in the direction of the rays of a strong light and move away from it (Fig. 13), but may react positively to a very weak light. The light causes gelation of the plasmasol ad-

joining the plasmagel, making it thicker and increasing the elastic strength of the portion illuminated. The response to light is thus due to the contraction of the plasmagel in the region stimulated, owing to the increase in the elastic strength of the plasmagel in this

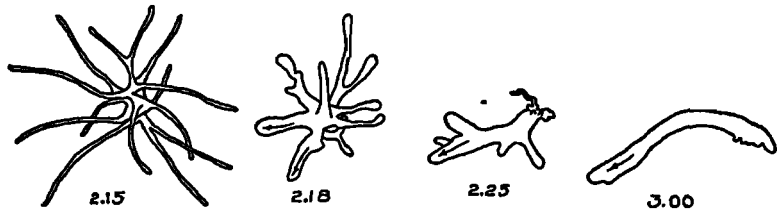


FIG. 12. — Changes in the shape of an amoeba when transferred from pure water to an N/1000 solution of NaCl. The numbers indicate the time of day and the arrows the direction of protoplasmic streaming in the pseudopodia. (After Mast.)

region. The evidence at present indicates that, while gelation or solation produced in a pseudopod of an amoeba by localized illumination is not followed by gelation or solation in other pseudopods, the effect of localized gelation and solation is transmitted, that *Amoeba* acts as an organized unit, and that its actions are, on

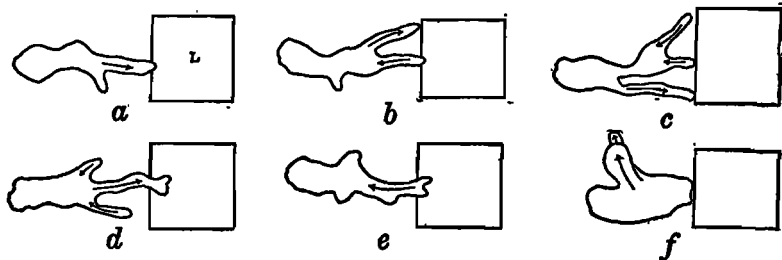


FIG. 13. — Reaction of an amoeba toward an area of intense light (L), the light rays of which were perpendicular to the slide. The successive positions of the amoeba are indicated at intervals of about one-half a minute. The arrows show the direction of protoplasmic streaming in the pseudopodia. (After Mast.)

the whole, adaptive. *Amoeba* responds to an electric current by moving toward the cathode; this results from the solation of the plasmagel on the cathodal side of the organism.

In amoeba there are no organs that can be compared with what we call sense organs in higher animals, and we must attribute its reactions to stimuli to that fundamental property of protoplasm called irritability. The superficial layer of cytoplasm receives the

stimulus and transfers the effects to some other part of the body; thus may be shown the phenomenon of *internal irritability* or *conductivity*. The stimulus causing a reaction seems to be in most cases *a change in the environment*. The behavior of amœba in the absence of external stimuli, for example when it is suspended freely in the water, shows that some of its activities are initiated by internal causes.

The reactions of amœba to stimuli are of undoubted value to the individual and to the preservation of the race, for the negative reaction is in most cases produced by injurious agents such as strong chemicals, heat, and mechanical impacts, whereas positive reactions are produced usually by beneficial agents. The responses, therefore, in the former cases carry the animal out of danger; in the latter, to safety.

Amœba is of fundamental interest to animal psychologists, since it represents the "*animal mind*" in its most primitive form. Whether or not the animal is in any degree conscious is a question still unanswered. If amœba has recognizable sensations, they must be infinitely less in both quality and quantity than those of higher organisms. That its behavior may be modified under experimental conditions has been demonstrated, which indicates that amœba may be able to learn by experience.

A review of the facts thus far obtained seems to show that factors are present in the behavior of amœba "comparable to the habits, reflexes, and automatic activities of higher organisms," and "if amœba were a large animal, so as to come within the everyday experience of human beings, its behavior would at once call forth the attribution to it of states of pleasure and pain, of hunger, desire, and the like, on precisely the same basis as we attribute these things to the dog." (Jennings.)

## (2) OTHER SARCODINA

**Order LOBOSA.** — The order LOBOSA contains amoeboid SARCODINA with lobose pseudopodia; there is no skeleton except a simple shell. Two suborders are usually recognized, — the GYMNAMOEBA, without a shell, and THECAMOEBA, with a shell.

*Amœba proteus* is the type of the class SARCODINA usually selected for detailed study and probably no other member of this class is as satisfactory for this purpose. However, many species of both free-living and parasitic SARCODINA may easily be secured

for observation that differ in various respects from the type. Some of these are described in the following paragraphs.

**Free-living amœbæ** (Fig. 14). — Several different species of amœba have been grouped together in the past under the name *Amœba proteus*. *Amœba proteus* was described by Leidy in 1879. It is characterized by the possession, in the younger forms, of a nucleus in the shape of a biconcave disk, which may become folded

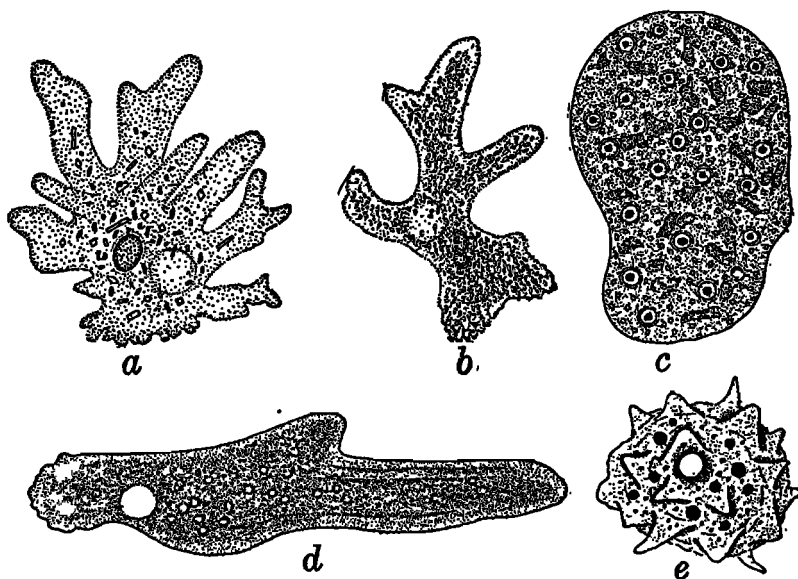


FIG. 14. — LOBOSA without shells. a, *Amœba dubia*, nucleus ovoidal. b, *Amœba discoides*; nucleus discoidal. c, *Pelomyxa palustris*; many nuclei. d, *Amœba carolinensis*; many nuclei. e, *Amœba verrucosa*; the tough pellicle results in many pseudopodia. (a, b, after Schaeffer; c, after Doflein; d, after Kepner and Edwards; e, after Wang.)

and convoluted in the older forms. It also has definite ectoplasmic ridges which are constant cell structures. A second form is much like the true *Amœba proteus* except that it possesses a disk-like nucleus which never becomes folded and its ectoplasm never shows the ridges constantly present in *Amœba proteus*. The name *Amœba discoides* has been given to this species (Fig. 14, b). A third form possesses an ovoid nucleus instead of a discoidal one and does not show any cytoplasmic ridges. Furthermore, it is characterized by a type of locomotion different from that of the

other species. To this form has been given the name *Amæba dubia* (Fig. 14, a). By means of carefully pedigreed cultures, Schaeffer has been able to show that these three forms breed true and probably represent true species. Another fairly common species is *Amæba verrucosa*, a sluggish form that has a tough pellicle and many short pseudopodia (Fig. 14, e). Some species of amœbæ have two nuclei and others, like *Amæba carolinensis* (Fig. 14, d), many nuclei.

To the genus *Pelomyxa* belong a number of fresh-water amœba-like species that contain two or more nuclei (Fig. 14, c). The characteristic feature of this genus is that the cytoplasm contains a number of refringent bodies which are of an albuminous nature and which are associated with a bacterial organism, *Cladothrix pelomyxa*. Furthermore, the organisms generally load their cytoplasm with sand and débris of all kinds in addition to food material. *Pelomyxa* reproduces itself asexually by simple fission and sexually by the formation of gametes. In some forms, the gametes are heliozoon-like with slender radiating pseudopodia; they conjugate in pairs. Each resulting organism develops into a young pelomyxa.

**Thecamœbæ.**—A number of common fresh-water genera belong to this suborder, including *Arcella*, *Diffugia*, *Centropyxis* (Fig. 15, g), *Lecquereusia* (Fig. 15, e), and *Euglypha*.

The arcellas possess a shell secreted entirely by the organism. This shell is arched above and has an opening in the center of the lower, flattened surface through which lobose pseudopodia are extended. *Arcella vulgaris* (Fig. 15, b) possesses two nuclei. *A. dentata* also has two nuclei, and a shell with dentate projections around the periphery (Fig. 15, c). *A. polypora* may contain as many as fifteen nuclei. In prepared specimens a large granular ring of protoplasm appears that stains deeply in hæmatoxylin; this is known as the chromidial body.

Arcellas can be reared in the laboratory quite easily. Pond weeds to which they are attached should be shaken vigorously in a large-mouthed bottle half full of water. The water should then be distributed to Syracuse watch glasses or petri dishes and kept covered at room temperature. Within a day or two, young arcellas may be found. Their shells are almost transparent, and nuclei, food bodies, and vacuoles can be seen clearly.

The commonest species of the genus *Diffugia* are *D. pyriformis*.

*D. lobostoma*, and *D. corona*. *D. pyriformis* has a bottle-shaped shell with a more or less distinct cylindrical neck (Fig. 15, *a*). *D. lobostoma* has a spherical or ovate shell with a lobed mouth opening. *D. corona* has a spherical shell with a variable number of spines at the end opposite the mouth opening (Fig. 15, *f*). A single nucleus is present.

The genus *Euglypha* contains several common species with a membranous shell composed of chitinous or siliceous plates, and teeth around the mouth opening. The pseudopodia are filiform.

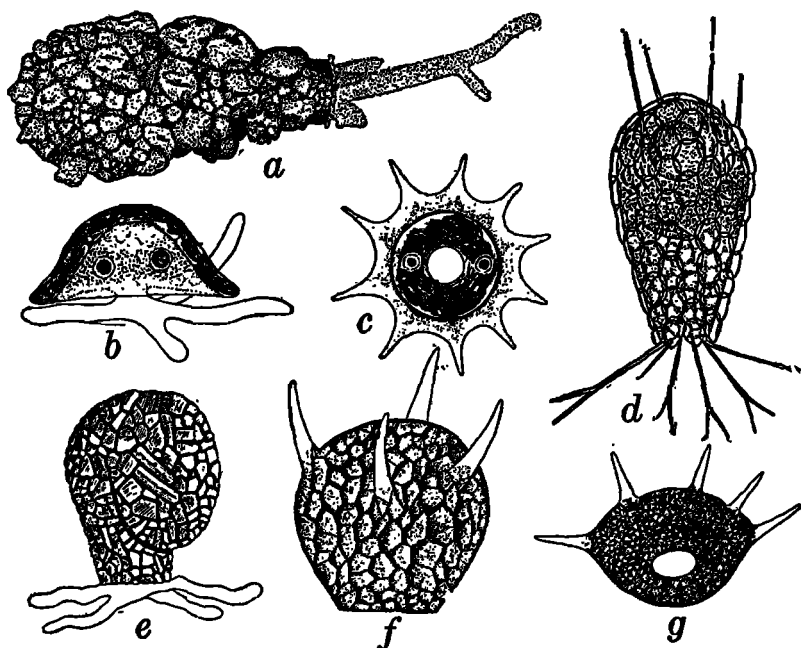


FIG. 15. — THECAMOEAE. Common species of shelled SÁRCODINA. *a*, *Diffugia pyriformis*. *b*, *Arcella vulgaris*. *c*, *Arcella dentata*. *d*, *Euglypha alveolata*. *e*, *Lecquereusia modesta*. *f*, *Diffugia corona*. *g*, *Centropyxis aculeata*. (*a*, after Reynolds; *b*, *c*, *e*, *f*, *g*, after Wang; *d*, after Calkins.)

*E. alveolata* usually has a few long spines (Fig. 15, *d*). *E. ciliata* has numerous smaller spines and is common in sphagnum moss.

Asexual reproduction in the THECAMOEAE takes place by binary fission, just as in the GYMNAMEAE, but is complicated by the presence of a shell. For example, in the case of *Diffugia corona* the organism prior to division accumulates a number of sand grains

within its interior. At the time of reproduction the protoplasm absorbs water, swells, and projects through the mouth of the shell. The projecting mass finally attains the size and assumes the shape of another *Diffugia*. The sand grains then rise to the surface, spread over it, and become embedded in a chitinous secretion which hardens and completes the formation of a new shell. By the time the new shell is formed, the nucleus has already di-

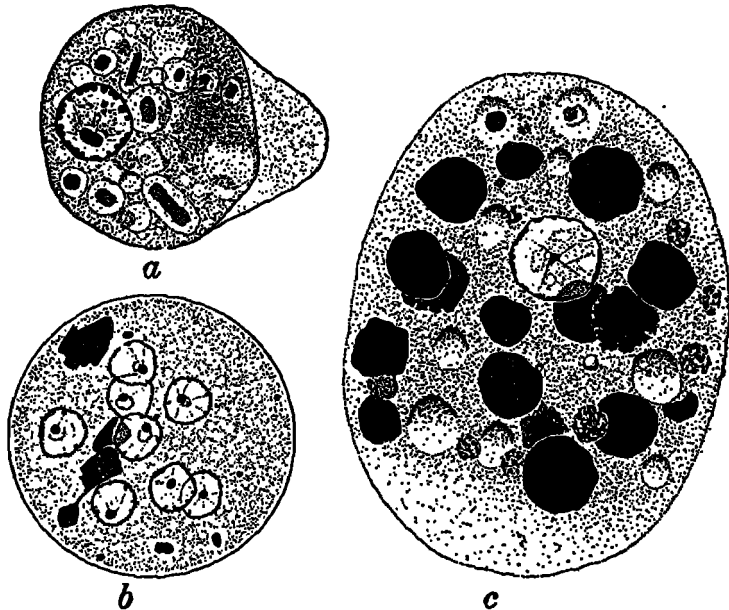


FIG. 16. — Amœbæ parasitic in the large intestine of man. *a*, *Endamoeba coli*, a harmless species, showing pseudopodium, nucleus and food vacuoles. *b*, *Endamoeba coli*, cyst containing 8 nuclei and a few chromatoid bodies (in black). *c*, *Endamoeba histolytica*, the organism of amoebic dysentery, containing a nucleus and many red blood corpuscles (in black). (After Stabler.)

vided and one of the daughter nuclei migrates into the newly protruded mass of protoplasm. Finally, the protoplasmic masses separate and two diffugias are formed, one inhabiting the old shell and the other the new shell.

**Parasitic amœbæ (Fig. 16).** — The SPOROZOA are always stated to be parasitic PROTOZOA and the impression may be made that all parasitic PROTOZOA belong to this class. The other three classes of PROTOZOA, however, include many parasitic species. Of special interest in the class SARCODINA are the parasitic amœbæ, particu-

larly those that occur in man. Human beings may be infected by as many as six species. One, *Endamæba gingivalis*, lives in the mouth in the tartar around the base of the teeth. Probably 50 per cent of the general population are infected. Specimens may be observed by scraping material from the base of the teeth and mounting it in 0.7 per cent NaCl solution. This amœba feeds principally on bacteria and leucocytes and is probably harmless al-

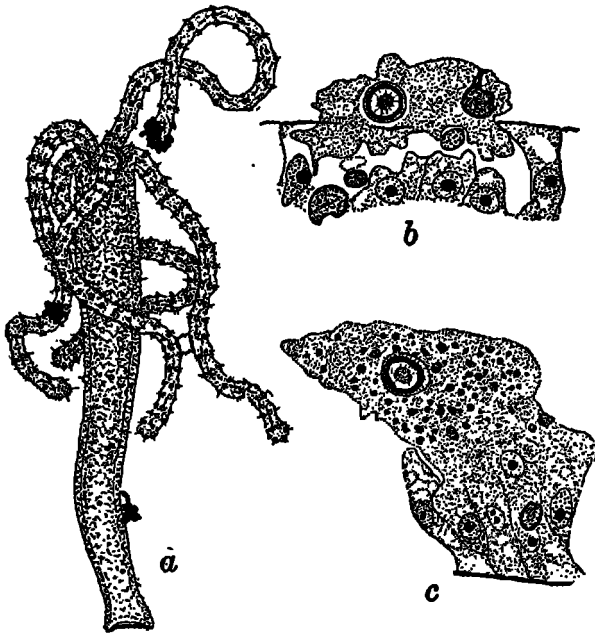


FIG. 17. — *Hydræmæba hydrozoena*: a parasite of *Hydra*. a, Four specimens (represented in black) on the surface of a hydra. b, An amœba destroying ectodermal cells. c, An amœba ingesting endodermal cells. (After Reynolds and Looper.)

though it is known to be present more frequently in diseased than in healthy mouths. Transmission occurs by contact during kissing.

The other five parasitic amœbæ of man live in the large intestine. One of them, *Endamæba histolytica* (Fig. 16, c), is pathogenic. The infective stage is a spherical cyst containing four nuclei. Encystment takes place in the large intestine and the cyst pass out in the faeces. Cysts that are swallowed in contaminated food or drink hatch in the small intestine giving rise to amœbæ with four nuclei, which subsequently divide into uninucleate amœbæ.



This species infects about 10 per cent of the general population but most of the infected persons are carriers, that is, the amœbæ live and multiply in their large intestine and produce cysts but do not injure them. In a few persons, however, the amœbæ attack the wall of the intestine producing ulcers and giving rise to amœbic dysentery. They seem to be particularly fond of red blood cells as a food supply. From the intestinal wall the amœbæ may be carried in the blood stream to the liver, lungs, brain, etc., where they sometimes produce abscesses. Drugs, such as emetine and yatren, are used successfully to cure amœbiasis.

The remaining four species of human amœbæ are supposed to be harmless. They are *Endamæba coli* (Fig. 16, a, b), *Endolimax nana*, *Iodamæba williamsi*, and *Dientamæba fragilis*. These amœbæ differ from one another especially in their nuclear structure. The last named frequently possesses two nuclei. The parasitic amœbæ resemble in general the free-living amœbæ but do not possess contractile vacuoles.

Practically every lower animal that has been carefully examined has been found to be infected with parasitic amœbæ. For example,

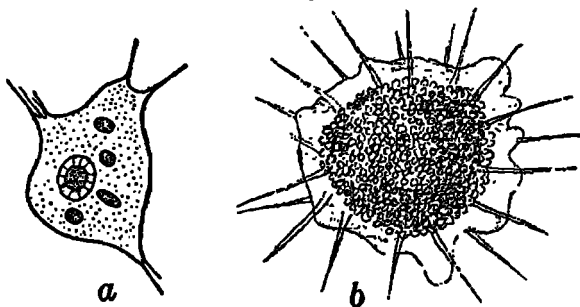


FIG. 18. — PROTEOMYXA. a, *Pseudospora volvocis*; amœboid stage of a parasite of *Volvox*. b, *Vampyrella lateritia*. (a, after Robertson; b, after Conn.)

*Hydramæba hydrozoena* (Fig. 17) is an amœba that occurs on the external surface and in the gastrovascular cavity of *Hydra*. It dies in from 4 to 10 days if removed from its host and is hence an obligate parasite. The hydras are injured by the amœbæ and usually are killed by them in about a week. Perhaps the parasitic amœbæ most easily obtained for study are those that occur in the intestine of the frog, frog tadpole, cockroach, and rat. Material containing parasitic Protozoa should always be diluted for study with a 0.7 per cent solution of NaCl instead of with water.

**Order PROTEOMYXA.** — This order contains a number of forms of very doubtful relationships, the only characters which they all possess in common being the absence of a shell and the formation of filose or reticulose pseudopodia.

An example of the PROTEOMYXA is *Pseudospora volvocis* (Fig. 18, a) which often parasitizes colonies of *Volvox*. It occurs in amœboid, flagellated, and heliozoan stages. In infected colonies of *Volvox* the amœboid stages can be seen creeping about and devouring the cell-individuals of its host. Another genus is *Vampyrella*. *V. lateritia* (Fig. 18, b) has a spherical body and is orange-red in color. It feeds on *Spirogyra* and other algæ.

**Order FORAMINIFERA** (Fig. 19). — All of the FORAMINIFERA possess shells, but the organisms differ from the THECAMEBÆ in

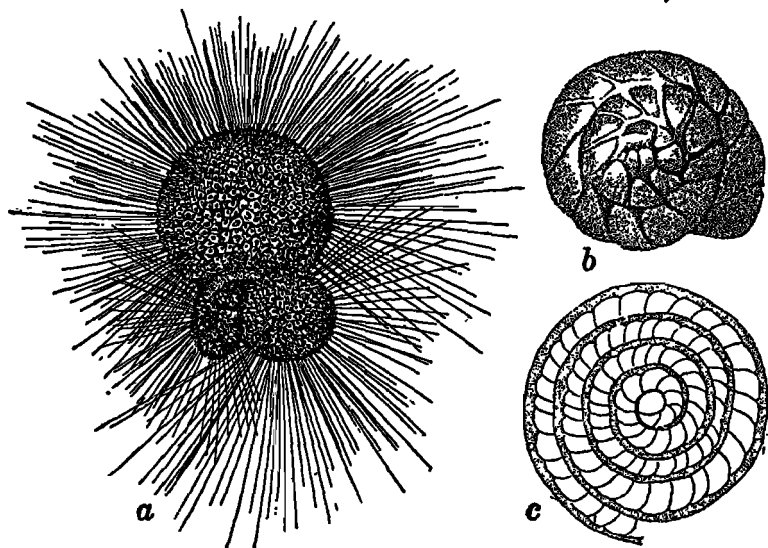


FIG. 19. — FORAMINIFERA. Shells of three species. a, *Globigerina bulloides*, with globular chambers and long spines. b, *Rotalia beccari*, upper surface showing chambers arranged in a helicoid spiral. c, *Nummulites lævigatus*, megalospheric form showing chambers in a spiral plane. (After several authors.)

that they form reticulose (rarely, filose) pseudopodia, which are used principally for capturing food. Shells secreted by the animal are generally chitinous or calcareous in nature, but a few are siliceous or gelatinous in composition. Some consist of foreign materials cemented together. They are generally divided into imper-

forate and perforate types, the former possessing a single opening through which the pseudopodia are protruded, just as in the case of the THECAMOEBAE, the latter possessing, in addition, a large number of fine pores through which the network of pseudopodia

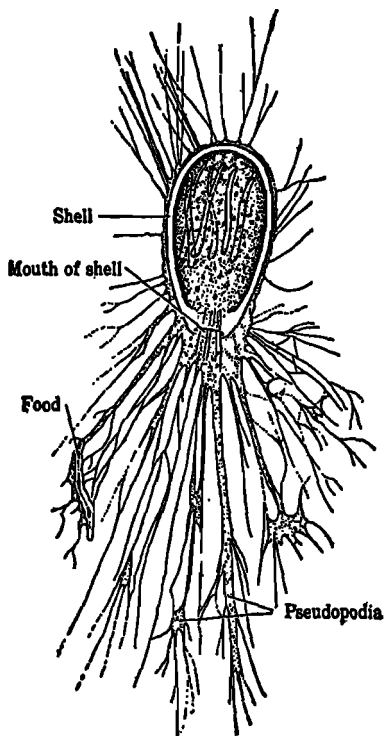


FIG. 20. — FORAMINIFERA. *Allogromia*, a fresh-water species, showing capture of food. (After Camb. Nat. Hist. from Woodruff.)

project. In the simpler FORAMINIFERA reproduction occurs by binary fission just as in the THECAMOEBAE. In the more complex forms, however, at the time of division the organisms do not separate but simply add another chamber to the shell structure. This gives rise to many-chambered shells. In the formation of such shells, each succeeding chamber is larger than the preceding one. The majority of the FORAMINIFERA are marine forms, although a few such as *Allogromia* (Fig. 20) occur in fresh water. Most of them live in the mud of the sea bottom and large areas in the Atlantic Ocean consist of globigerina ooze. So abundant are their shells that they form a large part of the white chalk laid down during the Cretaceous period and the nummulitic limestone of the Eocene (Fig. 19, c). *Globigerina bulloides* (Fig. 19, a) is a cosmopolitan species that is pelagic in habit and also lives in the mud at the bottom of the sea to depths of 3000 fathoms.

**Order HELIOZOA.** — The characteristics of this group may be stated as follows. The body is generally divided into two regions: (1) a cortical layer, which is alveolar in appearance, contains the contractile vacuole and gives rise to the pseudopodia, and (2) a medullary layer which contains the nuclear apparatus, food vacuoles, and, in some cases, symbiotic algæ. Many HELIOZOA possess

skeletons which may be either simple or complex in structure and may be composed of various materials. Asexual reproduction is effected by either binary fission or gemmation.

Two of the best-known species of HELIOZOA are *Actinophrys sol* and *Actinosphaerium eichhorni*. The former occurs among the vegetation in quiet, fresh water. It is spherical and small (about

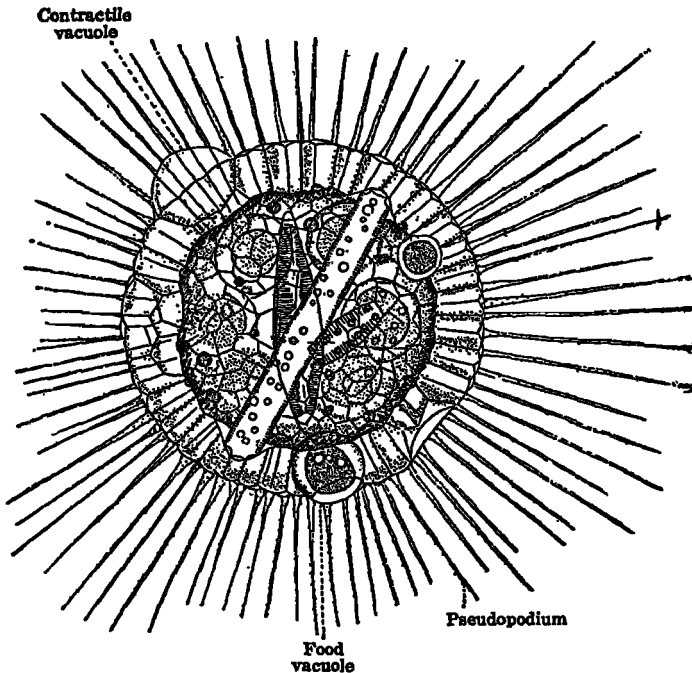


FIG. 21. — HELIOZOA. *Actinosphaerium eichhorni*. The endoplasm is crowded with food vacuoles containing diatoms, and nuclei are represented in the figure by the dark areas. (After Leidy.)

50 microns in diameter); has a large central nucleus; and possesses many large vacuoles in the ectoplasm. *Actinosphaerium eichhorni* (Fig. 21) is large, reaching one millimeter in diameter; has many nuclei in the outer layer of endoplasm and several contractile vacuoles. It is common among the plants in fresh-water ponds.

**Order RADIOLARIA** (Fig. 22). — The RADIOLARIA are exclusively marine and possess a central capsule, which is a membranous structure that divides the protoplasm of the body into an intra- and extracapsular region. The extracapsular region is itself divided into three layers. (1) The assimilative layer contains the

food, which is taken in by the pseudopodia, and various metaplastic granules. (2) The calymma contains a large number of vacuoles and is supposed to have a hydrostatic function. In some species this layer also contains a number of yellow symbiotic algæ

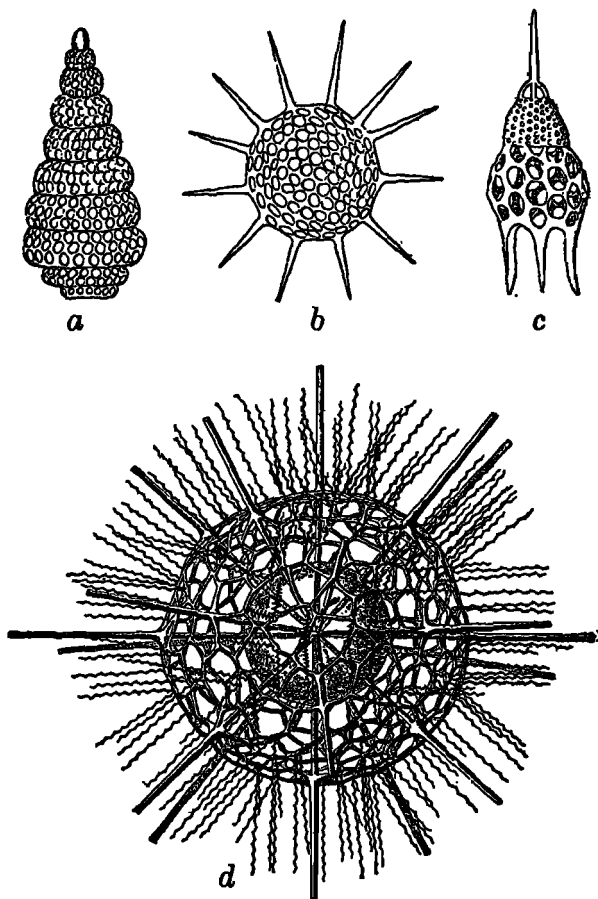


FIG. 22. — Radiolarian shells. a, *Lithocampe*, from the Devonian. b, *Trochodiscus*, from the Carboniferous. c, *Podocyrthis*, from the Tertiary. d, *Lichnaspis gillochii*. (a-c, after Woods; d, after Haeckel.)

(ZOOXANTHELLÆ). (3) The external layer surrounds the body and from it the pseudopodia arise. In the majority of species reproduction is associated with the formation of flagellated swarm spores which arise by a process of multiple fission within the intra-

capsular region. Most of the more than 4000 species live in the depths of the ocean.

## 2. CLASS II. MASTIGOPHORA

### (1) EUGLENA VIRIDIS

*Euglena viridis* is a favorable animal to represent the class MASTIGOPHORA. It is found in fresh-water ponds and may appear in cultures prepared for amœbæ. It is green in color, and, though a single animal cannot be seen with the naked eye, when a great many are massed together they impart a green tint to the water.

**Cytology** (Figs. 23, 24). — *Euglena* is a single elongated cell pointed at the posterior, and blunt at the anterior end. Two kinds of cytoplasm may be distinguished in *Euglena* as in *Amœba* and *Paramœcium*, a dense outer layer, the *ectoplasm*, and a central mass, *endoplasm*, which is more fluid. A thin *cuticle* is present, as in *Paramœcium*, covering the entire surface of the body. Parallel thickenings of this cuticle run obliquely around the animal, making it appear striated. A little to one side of the center of the anterior blunt end of the body is a funnel-shaped depression known as the *cytostome*. At the bottom of this depression is an opening which leads into a short duct called the *gullet*. This in turn enters a large spherical vesicle, the *reservoir*, into which several minute *contractile vacuoles* discharge their contents. The mouth and gullet are not used for the ingestion of food but as a canal for the escape of fluid from the reservoir.

A conspicuous structure in *Euglena* is the red eye spot or *stigma*. This is placed near the inner end of the gullet close to the reservoir. It consists of protoplasm in which are embedded a number of granules of hæmatochrome. The anterior end of the body of *Euglena* is said to be more sensitive to light than any other part, and it is supposed by some that the stigma functions as a rather primitive visual organ. This view is made probable by the presence of lens-like paramylum grains just anterior to it. The hæmatochrome also has many of the characteristics of the pigments in the eyes of higher organisms. If kept in the dark, *Euglena* soon loses its red pigment. A recent view is that the hæmatochrome shades a sensitive particle of protoplasm.

*Euglena* contains a single oval *nucleus* lying in a definite position a little posterior to the center of the body. It has a distinct

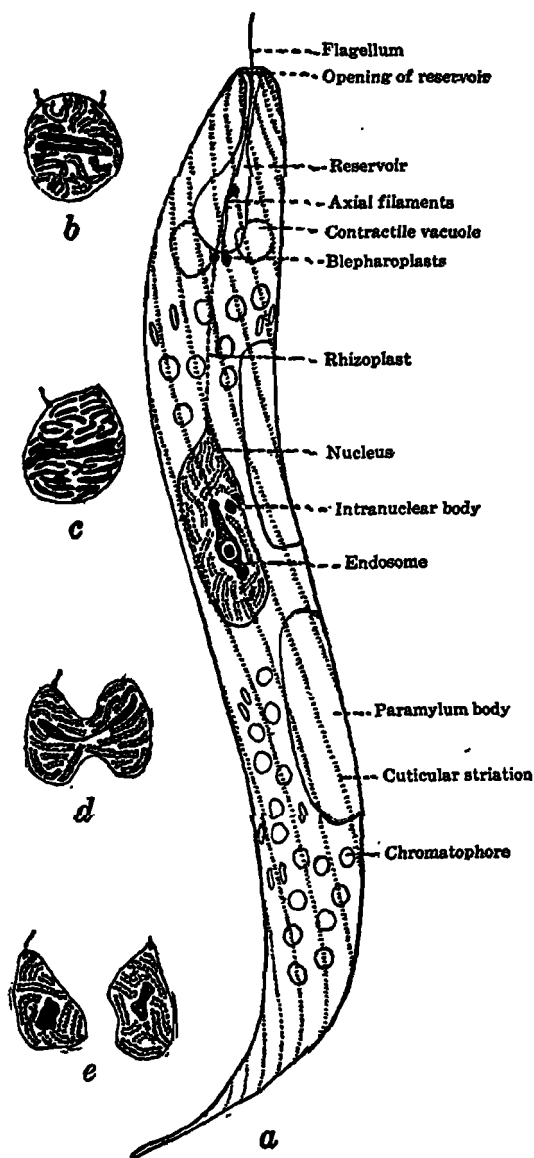


FIG. 23. — *Euglena spirogyra*: nuclear division. a, Vegetative form with nuclear chromatin in the form of paired rows of chromomeres. Only the proximal portion of the flagellum is included. b, Prophase nucleus. The chromosomes are in pairs; the endosome has elongated and divided into two; the axial filaments are attached to two blepharoplasts on the nuclear membrane that have arisen from the intranuclear body. c, Metaphase nucleus. The chromosomes separate and the endosome elongates. d, Anaphase nucleus. The nuclear membrane constricts; the chromosomes divide longitudinally and become granular; and the endosome constricts. e, Nuclear division completed. The nuclei next assume the appearance indicated in a. (After Ratcliffe.)

membrane, and contains a central body which is called an *endosome*; this body functions as a division center during mitosis.

*Euglena* derives its green color from a number of oval disks suspended in the protoplasm. These are known as *chromatophores*. They are arranged about a collection of granules situated in the center of the body, and contain chlorophyll, which is diffused throughout their protoplasmic contents. They manufacture food by a process common in green plants but rare in animals, called photosynthesis.

When properly fixed and stained a number of bodies appear within *Euglena* that are not visible in the animal when alive or when prepared for study by the usual methods. Some of these bodies are illustrated in figure 24. They include the chondriome, pseudochondriome, plastidome, and Golgi bodies. The relations of these protoplasmic inclusions to the functions of the *Euglena* are more or less problematical.

**Nutrition.** — Although *Euglena* has a mouth and gullet, it is very doubtful, as noted above, if any food is ingested.

Food is manufactured as in green plants, by the aid of the chlorophyll in the chromatophores. This mode of nutrition is known as

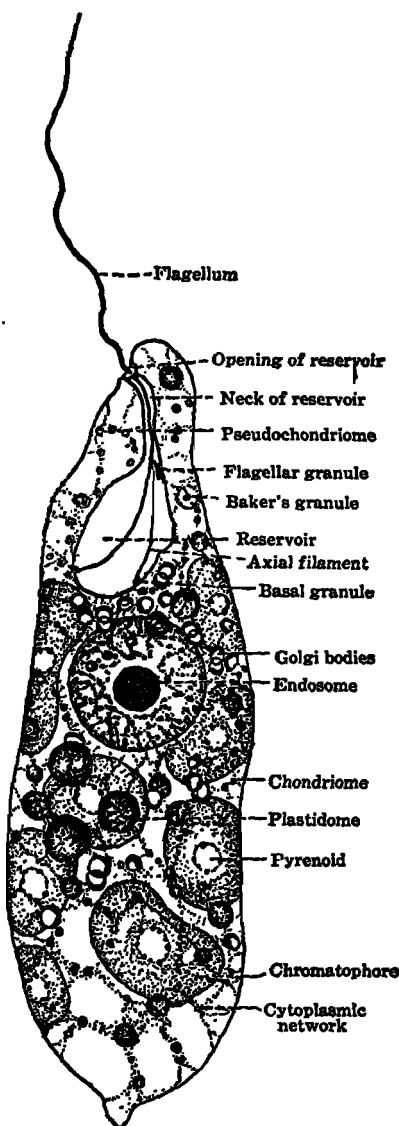


FIG. 24. — *Euglena gracilis*. Diagram of a specimen showing various cytoplasmic inclusions. (After Brown.)



*holophytic*. The chlorophyll is able, in the presence of light, to break down the carbonic acid ( $\text{CO}_2$ ), thus setting free the oxygen, and



FIG. 25. — Flagellum. The solid line is the elastic core or axial filament which is surrounded by a protoplasmic sheath. (After Plenge.)

to unite the carbon with water, forming a substance allied to starch called paramylum. If specimens are kept in good light continually,

a large amount of paramylum will be stored up for future use, being laid down around some granules of protein substance near the center of the body. These granules are called *pyrenoids*.

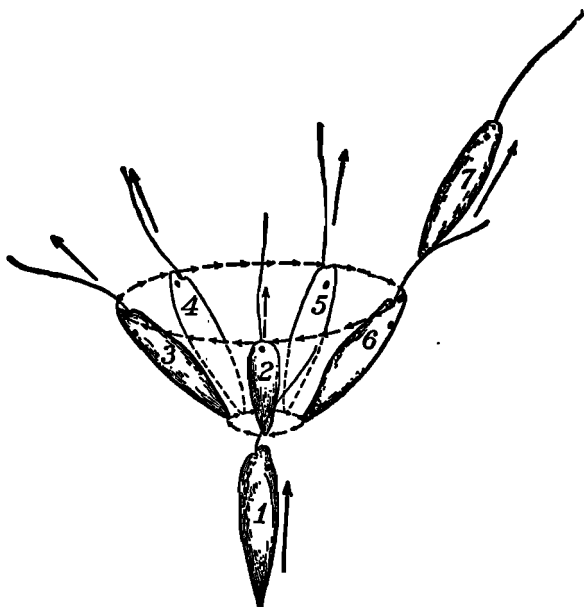


FIG. 26. — *Euglena*: reaction to light. The organism is swimming forward at 1; when it reaches 2 it is shaded. It thereupon swerves toward the dorsal side, at the same time continuing to revolve on the long axis, so that its anterior end describes a circle, the *Euglena* occupying successively the positions 2-6. From any of these it may start forward in the directions indicated by the arrows. (From Jennings.)

Both the pyrenoids and chromatophores are permanent cell structures and increase in number by division and not by the origin of new ones from the other parts of the body. That all the food necessary for the life of *Euglena* is not procured by photosynthesis is shown by the fact that the animal is able

to live in the dark for over a month, whereas chlorophyll demands light before the production of paramylum is possible. This seems to indicate that organic substances in solution are absorbed through the surface of the body, that is, saprophytic nutrition supplements the holophytic. The nutrition of *Euglena* differs from that of the majority of animals, since the latter live by ingesting solid particles of food and are said to be *holozoic*. By some authorities *Euglena* is regarded as a plant and placed in the plant series among the unicellular algæ since it contains chlorophyll, a substance characteristically present in plants. Others regard *Euglena* as an animal that has acquired a plant-like type of nutrition.

**Locomotion.**—*Euglena* changes its shape frequently, becoming shorter and thicker, and shows certain squirming movements. These prove that it possesses considerable elasticity, since the normal shape is regained if enough water is present. Often in a favorable specimen, a thread-like structure may be seen projecting from the anterior end of the body and bending to and fro, drawing the animal after it. This is the *flagellum* (Fig. 25). It is more or less cylindrical and possesses a central rod-like elastic core and a much more fluid protoplasmic sheath. If the flagellum cannot be seen in the living animal, a little iodine placed under the cover glass will help to bring it out.

**Behavior.**—*Euglena* swims through the water in a spiral path. The effect of this is the production of a perfectly straight course through the trackless water. When stimulated by a change in the intensity of the light, *Euglena*, in the majority of cases, stops or moves backward, turns strongly toward the dorsal side, but continues to revolve on its long axis. The posterior end then acts as a pivot while the anterior end traces a circle of wide diameter in the water. The animal may swim forward in a new direction from any point in this circle. This is the *avoiding reaction* (Fig. 26).

*Euglena* is very sensitive to light (Fig. 27). It swims toward an ordinary light such as that from a window (Fig. 28), and if a cul-

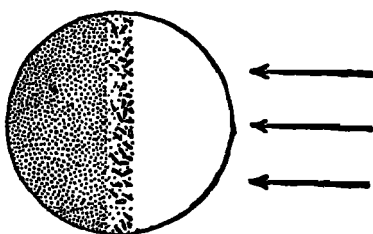


FIG. 27. — *Euglena*: reaction to light. The light comes from the direction indicated by the arrows, while the opposite side of the vessel is shaded, as indicated by the dots. The euglenæ gather in the intermediate region across the middle. (From Jennings.)

ture containing euglenæ is examined, most of the animals will be found on the side toward the brightest light. This is of distinct advantage to the animal, since light is necessary for the assimilation of carbon dioxide by means of its chlorophyll. *Euglena* will swim away from the direct rays of the sun. Direct sunlight will kill the organism if allowed to act for a long time. If a drop of water containing euglenæ is placed in the direct sun-

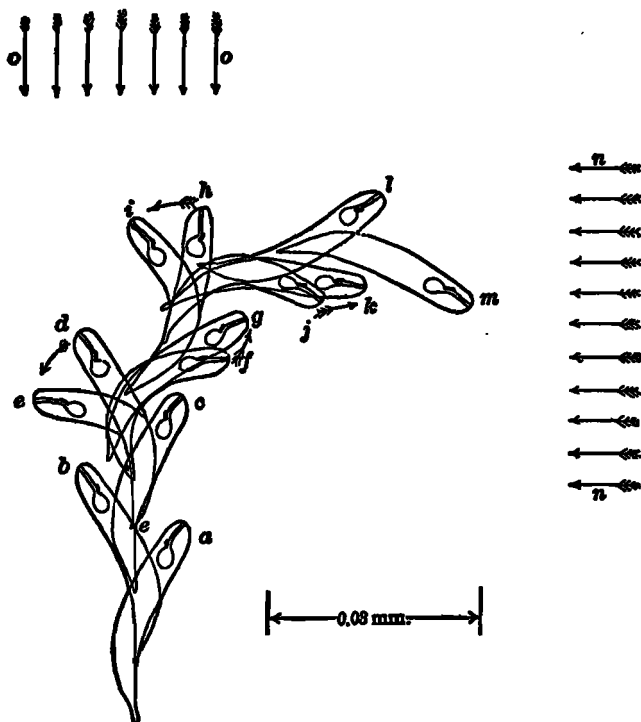


FIG. 28. — Orientation of *Euglena* in the direction of light rays. *a-c*, positions when light rays were coming from direction *o*; *e-m*, positions when the *o* rays were cut off and the *n* rays turned on. (After Mast.)

light and then one half of it is shaded, the animals will avoid the shady part and also the direct sunlight, both of which are unfavorable to them, and will remain in a small band between the two in the light best suited for them, that is, their optimum. By shading various portions of the body of a *Euglena* it has been found that the region in front of the eye spot is more sensitive than any other part. It should be noted that when *Euglena* is swimming

through the water it is this anterior end which first reaches an injurious environment; the animals give the avoiding reaction at once, and are thus carried out of danger.

**Reproduction.** — Reproduction in *Euglena* takes place by binary longitudinal division (Fig. 29, a). Nuclear division takes place within the nuclear membrane (Fig. 23). The chromatin, which is in the form of paired strands of chromomeres in the vegetative stage, form pairs of chromosomes each of which divides longitudinally into two. The endosome becomes constricted into two approximately equal parts. The intranuclear body also divides into two and these give rise to the blepharoplasts. The body begins to divide at the anterior end. The old flagellum is retained by one

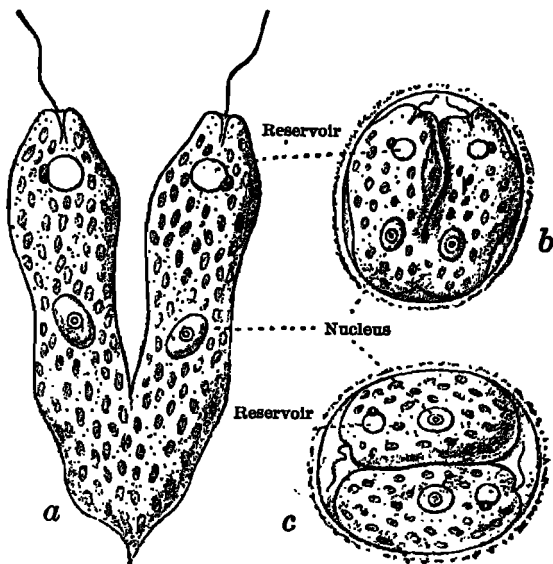


FIG. 29. — *Euglena viridis*: reproduction. a, Binary longitudinal fission. b, c, Binary division within a cyst. (After Stein, from Bourne.)

half, while a new flagellum is developed by the other. Often division takes place while the animals are in the encysted condition. Occasionally euglenæ are found which have become almost spherical and are surrounded by a rather thick gelatinous covering which they have secreted (Fig. 29, b, c). Such an animal is said to be encysted. In this condition periods of drought are successfully passed, the animals becoming active when water is again encountered. Usually in cultures brought into the laboratory many cysts are found on the sides of the dish. Encystment frequently takes place without any apparent cause, the animal resting in this condition for a time and then emerging again to its free-swimming habit. Before encystment the flagellum is thrown off,

a new one being produced when activity is again resumed. One cyst usually produces two euglenæ although these may divide while still within the old cyst wall, making four in all, while certain observers have recorded as many as thirty-two young flagellated euglenæ which escaped from a single cyst.

## (2) OTHER MASTIGOPHORA

The class MASTIGOPHORA includes a very large number of minute PROTOZOA that are rather difficult to classify, hence the taxonomy of the group is in a chaotic state. It is convenient to separate them into two subclasses, (1) plant-like species or PHYTOMASTIGINA and (2) animal-like species or ZOOMASTIGINA. Certain of the more common and interesting species will be referred to under the orders usually recognized in these two subclasses.

### Phytomastigina

**Order CHRYSOMONADIDA.** — This order includes a number of small forms which typically contain one or two brownish chromatophores and one or two flagella; these flagella may be equal in size or differentiated into a principal and accessory one. The body is often amœboid and food may even be taken in by pseudopodia. Nutrition is either holophytic or holozoic or both.

**Protozoa of drinking water.** — Several species of CHRYSOMONADIDA are of particular interest because they sometimes become very numerous in water confined in reservoirs and render it unfit for drinking purposes. They are all colonial in habit. *Uroglena americana* (Fig. 30, a) forms spherical colonies the individuals of which are embedded in the periphery of a gelatinous matrix. A stigma and plate-like chromatophore are present. *Dinobryon sertularia* (Fig. 30, b) has a vase-like, hyaline, or yellowish cellulose test, usually a stigma and one or two brownish chromatophores. *Synura uella* (Fig. 30, c) consists of from 2 to 50 individuals arranged in radial fashion; each has a stigma and two brown chromatophores. *Uroglena* is said to be the worst of the species, giving rise to a fishy odor; when large numbers are present an odor resembling cod liver oil results. *Dinobryon* also produces a fishy odor. *Synura* is responsible for an odor resembling ripe cucumbers and a bitter and spicy taste. These odors are due to aromatic oils elaborated by the organisms during growth and

liberated when they die and disintegrate. They are recognizable when present in minute amounts; for example, the oil of *Synura* produces a perceptible odor in a dilution of one part of oil to twenty-five million parts of water. Treating water with copper

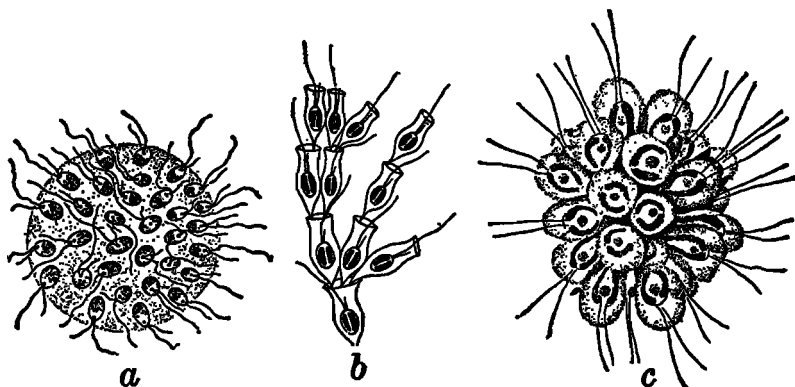


FIG. 30. — CHRYSOMONADIDA. Colonial flagellates sometimes obnoxious in drinking water. a, *Uroglena americana*. b, *Dinobryon sertularia*. c, *Synura wella*. (After various authors.)

sulphate kills these PROTOZOA and brings about the disappearance of the odors.

**Order CRYPTOMONADIDA.** — *Chilomonas paramecium* (Fig. 31, b) is a common species belonging to this order, — one that frequently occurs in laboratory cultures. It is about 35 microns in length, without chromatophores and hence colorless, with two anteriorly directed flagella, a contractile vacuole on one side near the anterior end, a spherical nucleus posterior to the center, and a mass of endoplasm that is distinctly alveolar in structure. No solid food particles are ingested but nutritive substances are absorbed through the surface of the body. Reproduction is by longitudinal fission; the nucleus divides, then the body divides into two and new flagella grow out.

**Order DINOFLAGELLIDA** (Fig. 31, a). — The most characteristic features of the DINOFLAGELLIDA are their shell and flagellar apparatus. The shell or lorica is a rigid structure, sometimes very bizarre in form, composed of cellulose, or an allied substance, which usually has a longitudinal groove or sulcus, and a circular groove or girdle. Two flagella are present which issue from pores in the lorica and lie within these grooves. The majority of species

are holophytic and possess chromatophores which may be brown, pale green, or yellow. A few species, however, have taken on a holozoic method of nutrition and may even ingest their food by pseudopodia. Frequently a stigma is present. Asexual reproduction by fission takes place.

Most of the dinoflagellates are salt-water species; a large number are parasites, and many live in fresh water. Among the fresh-water

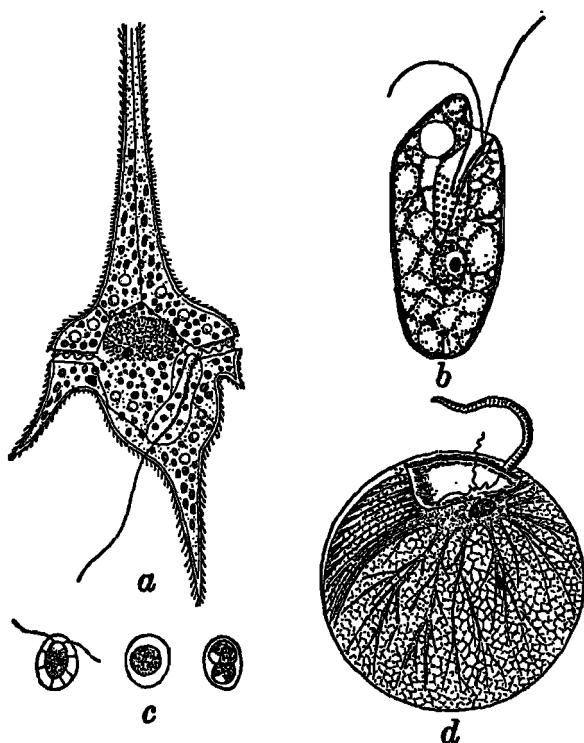


FIG. 31.—PHYTOMASTIGINA. a, DINOFLAGELLIDA; *Ceratium macroceras*. b, CRYPTOMONADIDA; *Chilomonas paramecium*. c, PHYTOMONADIDA; *Hematococcus lacustris*. Active, resting, and division stages. d, DINOFLAGELLIDA; *Noctiluca scintillans*. (After various authors.)

species are *Peridinium tabulatum* and *Ceratium hirudinella*. An interesting marine species is *Noctiluca scintillans* (Fig. 31, d). It is spherical in shape, bilaterally symmetrical and usually from 500 to 1000 microns in diameter. It possesses a small flagellum and a tentacle, and cytoplasm that is much vacuolated. Sometimes

noctilucae are so abundant in the Atlantic and Pacific as to color the water red by day and render it phosphorescent by night.

**Order PHYTOMONADIDA.** — The members of this order are undoubtedly closely allied to the algæ. The body is covered with a rigid cellulose membrane. Biflagellate forms are typical, the flagella being inserted through pores in the cellulose wall. By far the great majority of the species are exclusively holophytic and possess a large cup-shaped green chromatophore. A few colorless forms which live saprophytically are referred to this order, but in no case do any of the forms ingest solid food. A red stigma or eye spot is also present. Asexual reproduction takes place giving rise to numbers of small flagellated swimmers. Sexual phenomena are definitely known for a large number of species. Colony formation is quite frequent. Among the interesting species are *Hæmatococcus lacustris* (Fig. 31, c) which is colored red and when present in large numbers is responsible for "red rain" and "red snow," and a group of types belonging mostly to the family VOLVOCIDÆ which can be arranged in such a way as to illustrate the evolution of multicellular from unicellular organisms and also the evolution of sex as indicated in the following paragraphs and in figures 32 and 33.

*Spondylomorom* (Fig. 32, a) is colonial in habit with sixteen cells in each colony. These cells are practically independent. Each of them reproduces by fission to form a colony like the parent colony. No gamete formation is known.

*Chlamydomonas* (Fig. 32, b) is a unicellular type that reproduces vegetatively by fission into two, four, or eight daughter cells and also produces gametes all of one size which fuse together in pairs forming zygotes; these zygotes undergo fission resulting in a number of vegetative unicellular individuals.

*Pandorina* (Fig. 32, c) is a colonial form of sixteen cells embedded in a gelatinous matrix, each independent of the others. New colonies are produced by each cell by fission. Gametes are also formed, some being larger than others. The larger appear to fuse with the smaller to form zygotes, and since sexual reproduction consists in the fusion of a larger female gamete with a smaller male gamete, the process in *Pandorina* seems to furnish an early stage in the evolution of sex.

*Eudorina* is a colonial type with thirty-two cells. Each cell may reproduce a colony vegetatively by fission. At times the cells



of certain colonies become large; this is characteristic of female colonies and the large cells are macrogametes. In other male colonies each cell divides to form sixteen or thirty-two microgametes. The microgametes fuse with the macrogametes in pairs to

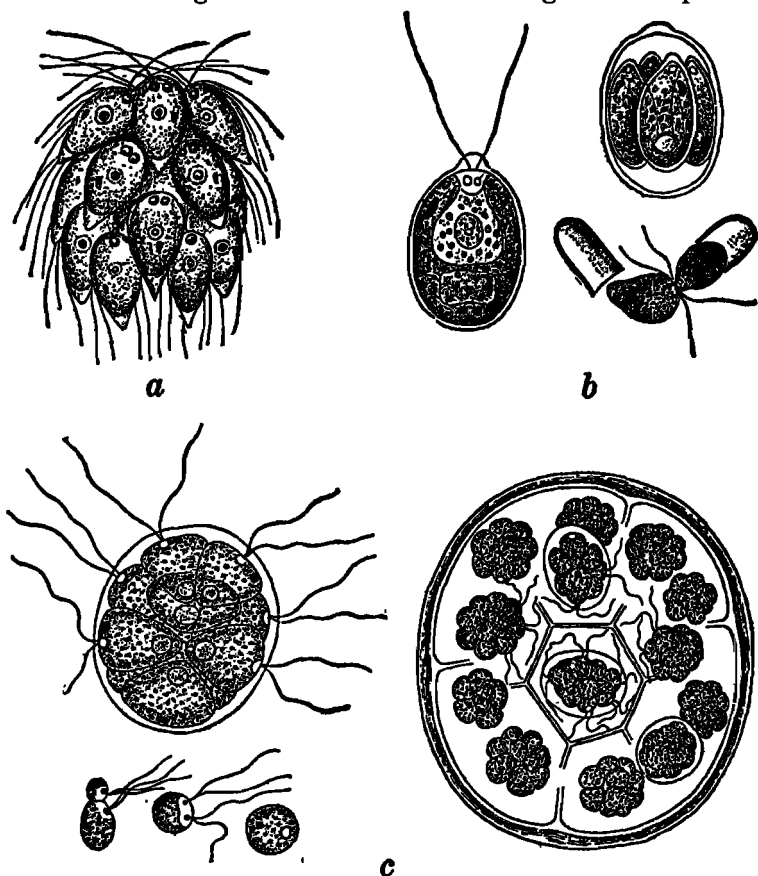


FIG. 32. — COLONIAL PHYTOMONADIDA. a, *Spondylomorom quaternarium*. b, *Chlamydomonas monadina*; active, dividing, and fusion of gametes. c, *Pandorina morum*; active, dividing, and fusion of gametes into a zygote. (After Oltmanns.)

form zygotes. In this species there is no doubt about the difference in size between the conjugating gametes.

*Volvox globator* (Fig. 33) represents the final stage in the series. The thousands of vegetative cells in a colony are united by protoplasmic strands; physiological continuity is thus established be-

tween the cells, a condition not found in the colonies previously described. Most of the cells contain an eye spot, chlorophyll, a contractile vacuole, and two flagella. These are called "body" or somatic cells. The production of daughter colonies is accomplished by special reproductive cells which are set aside for this purpose. The asexual method is as follows. Certain cells of the colony are

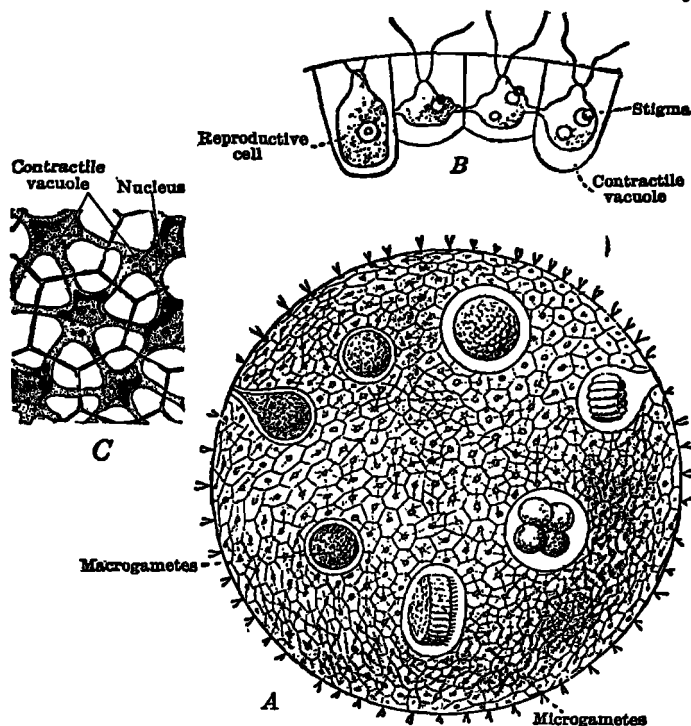


FIG. 33. — *Volvox globator*: a large colonial flagellate. A, a sexually ripe colony, showing microgametes and macrogametes in various stages of development. B, a portion of the edge of the colony highly magnified, showing three flagellate cells united by protoplasmic strands, and a single reproductive cell. C, a single cell connected with surrounding cells by protoplasmic strands. (After K  lliker, from Bourne.)

larger than others and lack flagella; a number of these in one colony increase in size, and divide by simple fission into a great number of cells, producing new colonies without being fertilized. The cells that act in this way are named parthenogonidia. The sexual method of reproduction may be observed in colonies which contain as many as fifty of the larger non-flagellated cells. Some of these

grow larger and may be recognized as female cells or macrogametes; others produce by simple division a flat plate, containing about 128 spindle-shaped male cells or microgametes. These fuse with the macrogametes. The zygote thus formed secretes a surrounding wall and in this condition the winter is passed. The following spring the zygote breaks out of the wall and by division produces a new colony. The smaller somatic cells contained in the mother colony fall to the bottom and disintegrate as soon as the new colonies produced by the fertilized germ cells have escaped.

In *Volvox*, true somatic cells are encountered for the first time, that is, cells which function only vegetatively and are unable to

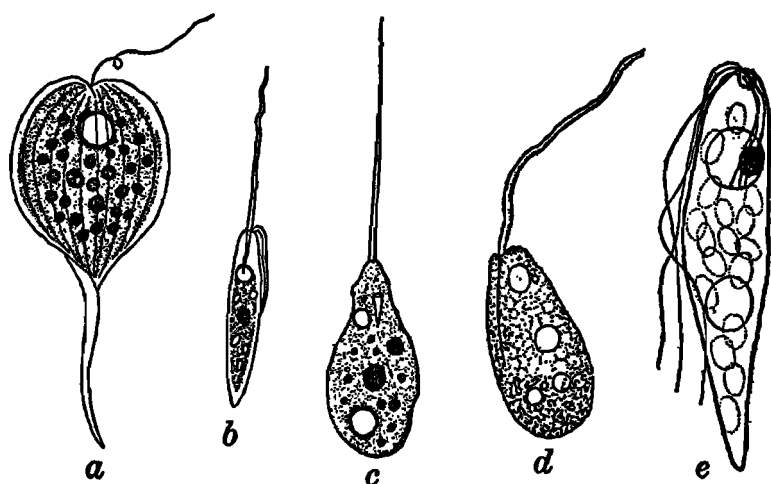


FIG. 34. — EUGLENOIDIDA. a, *Phacus longicaudus*. b, *Heteronema acus*. c, *Peranema trichophorum*. d, *Copromonas subtilis*. e, *Euglenamorphia hegneri*. (After various authors.)

reproduce the colony. In the other forms described every cell has the capacity of reproducing the whole. *Volvox* also contains true germ cells, that is, cells that have given up nutritive functions to carry on reproduction. Furthermore, a clear case of natural death occurs in the somatic cells when they fall to the bottom of the pond and disintegrate. The bodies of higher animals consist of many cells which may be separated into somatic and germ cells. The latter are either male or female. In most cases the fusion of a male cell with a female cell is necessary before a new animal can be reproduced. At any rate, some of these germ cells maintain the

continuation of the species by producing new individuals while the somatic cells perish when the animal dies.

**Order EUGLENOIDIDA.** — This order contains flagellates that are comparatively large. *Euglena* is a rather typical genus and *E. viridis* presents the principal characteristics of the group (page 31). A number of interesting species are common in fresh water. *Euglena pisciformis* is a highly active spindle-shaped species. *E. spirogyra* is large and sluggish. *E. sanguinea* has a hæmatochrome. The genus *Phacus* (Fig. 34, *a*) is represented by several fresh-water species. The body is much flattened and the cuticle has conspicuous striations. Green chromatophores are present. *Peranema trichophorum* (Fig. 34, *c*) is a common species. Its body is broad and truncated at the posterior end when in locomotion and a long flagellum with vibrating tip extends out from the pointed anterior end. The body is very plastic when stationary. *Heteronema acus* (Fig. 34, *b*) occurs in fresh water and in the soil. Two flagella arise from the anterior end one directed forward and the other backward. The body is colorless, plastic, and pointed at both ends.

*Copromonas subtilis* (Fig. 34, *d*) is an interesting species because it is coprozoic, that is, it occurs in the fæces of higher animals which it finds a favorable environment. It has been recorded from the fæces of frogs, toads, pigs, and man. A parasitic species, *Euglenamorphia hegeneri* (Fig. 34, *e*), that occurs commonly in the intestine of frog and toad tadpoles probably belongs to this group, and, if so, is the only representative which possesses three flagella. It lives between the food mass and the wall of the intestine or rectum of tadpoles and can be transferred from one tadpole to another of the same or different species either by the association of infected tadpoles with clean tadpoles or by the feeding of clean tadpoles with the rectum from infected animals.

### Zoomastigina

**Order PANTASTOMATIDA** (Fig. 35, *c*). — This order is characterized by the fact that the organisms ingest their food at any point on the body by means of pseudopodia. They exhibit so many transitional characters between the true SARCODINA on the one hand and the MASTIGOPHORA on the other that it is exceedingly difficult to define their exact relationships. A common species in fresh water and soil is *Mastigamæba aspera*. This species has a single long flagellum and pushes out finger-like pseudopodia.

*Mastigina hylæ* is a parasitic species that occurs in the large intestine of frog tadpoles. A short, inactive flagellum arises from the nucleus at the anterior end.

**Order PROTOMONADIDA.** — This order comprises a vast number of flagellates generally of small size, and is particularly interesting because it includes many of the flagellates living in man. The members of the group generally possess a very thin cuticle, a weakly amœboid body, and from 1 to 6 flagella arranged in various ways. Forms which are holozoic ingest their food at a definite

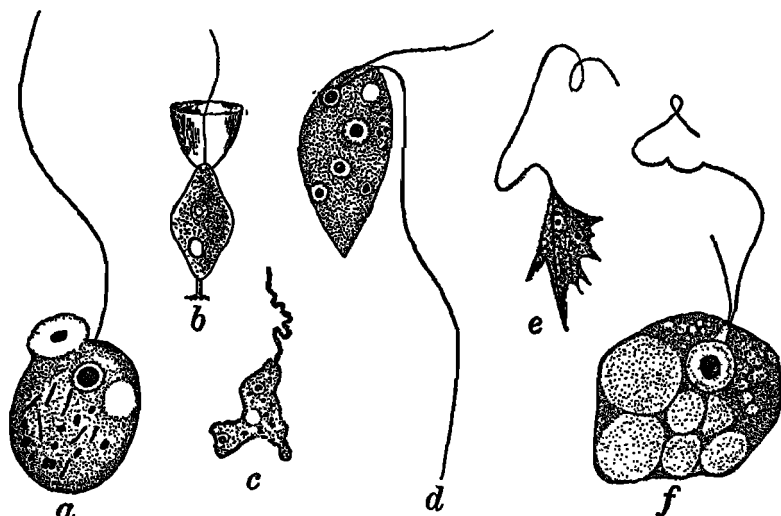


FIG. 35. — ZOOMASTIGINA. a, *Oikomonas termo*. b, *Monosiga brevipes*. c, *Mastigamœba invertens*. d, *Bodo sallans*. e, *Cercomonas longicauda*. f, *Monas vulgaris*. (After various authors.)

place on the body (generally at the base of the flagellum) where a cytostome may be present. In the parasitic forms undulating membranes may occur. Asexual reproduction takes place by longitudinal fission.

Of the free-living PROTOMONADIDA, *Oikomonas termo* (Fig. 35, a) is a simple type that is often common in fresh water and soil. It is very small (4 to 5 microns in diameter), spherical in shape, and has a single long flagellum. Another fresh-water species is *Monosiga brevipes* (Fig. 35, b). This is a representative of the choanoflagellates which have a delicate collar around the flagellum. *Bodo caudatus*, *Cercomonas longicauda* (Fig. 35, e), and *Monas*

*vulgaris* (Fig. 35, *f*) are very common in stagnant water and infusions and the first two are often coprozoic. *Bodo* (Fig. 35, *d*) is ovoid and plastic with two anterior flagella, — one directed forward, the other trailing behind, and a spherical nucleus near or anterior to the center of the body. *Cercomonas* is similar to *Bodo* but the trailing flagellum is attached to the side of the body and the nucleus is pyriform. *Monas* has two anterior flagella directed forward, one a longer primary flagellum and the other a shorter secondary flagellum.

The five genera of parasitic species described below are obviously closely related. They are usually grouped together as blood-inhabiting flagellates to distinguish them from another group that live in the digestive tract and are called intestinal flagellates. During its life cycle *Trypanosoma* may assume trypanosome, crithidial, herpetomonad, and leishmania stages; *Herpetomonas* may appear in trypanosome, herpetomonad, crithidial, and leishmania stages; *Crithidia* in crithidial, herpetomonad, and leishmania stages; and *Leishmania* in herpetomonad and leishmania stages.

The genus *Trypanosoma*. — The trypanosomes are widely spread among animals. They occur in man, many other mammals, birds, reptiles, amphibians, and fish. The type species, *T. rotatorium* (Fig. 36, *a*), occurs in the blood of frogs and is not uncommon in this country. Another species, *T. diemyleti* (Fig. 36, *b*), is present in the blood of the common crimson-spotted newt, *Triturus viridescens*, in certain localities. Specimens may be obtained by snipping off the end of the tail and mounting a drop of blood on a slide. Permanent preparations are made by spreading the blood on the slide as a film, allowing it to dry and staining by the Romanowsky method. Three species are known from man; *T. gambiense* the organism of Gambian sleeping sickness and *T. rhodesiense* of Rhodesian sleeping sickness are localized in Africa: and *T. cruzi* of Chagas' disease in South and Central America. The African types live also in wild game, such as antelope, and are transmitted by tsetse flies; the American type occurs especially in armadillos which serve as reservoirs from which the transmitting agents, the triatoma kissing bugs, may acquire their infection. All human trypanosomes are pathogenic and frequently bring about the death of the host.

Animal trypanosomes are mostly non-pathogenic. *T. lewisi* of the wild rat is a good example of this type. Among the more

important trypanosomes that cause disease in lower animals are *T. equiperdum*, the organism of the disease of horses known as dourine; *T. brucei*, the organism of nagana in various domesticated animals; *T. evansi*, of surra in domesticated animals; *T. equinum*, of mal-de-caderas in horses and mules; and *T. hippicum*, of murrina in horses and mules. Trypanosomes are often local in their distribution, that is, many species are limited to the animals in certain definite geographical areas. This is due primarily to the fact that the transmitting agents are geographically restricted. For the most part, the transmitting agents of trypanosomes of terrestrial animals are blood-sucking insects and those of aquatic animals are blood-

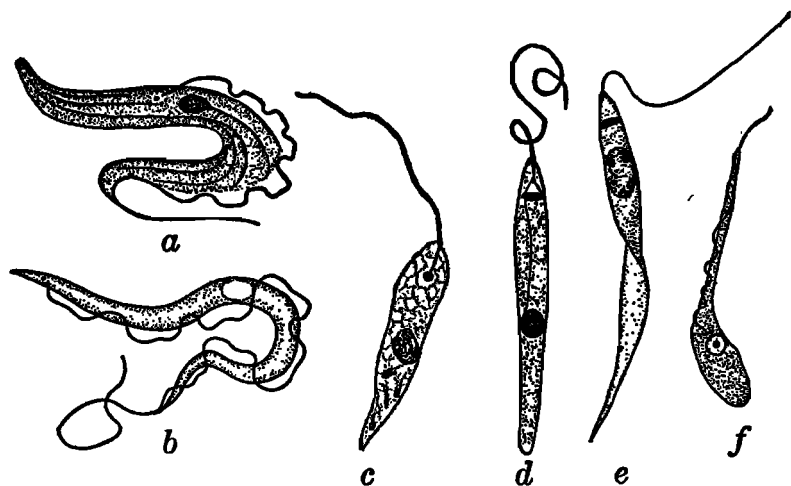


FIG. 36. — PROTOMONADIDA. a, *Trypanosoma rotatorium*, from the frog. b, *Trypanosoma diemyctyli*, from the newt. c, *Leishmania donovani*, from man. d, *Herpetomonas muscarum*, from the house fly. e, *Phylomonas elmassiani*, from the milkweed plant. f, *Crithidia gerridis*, from the water strider. (After various authors.)

sucking leeches. The transmitting agents are usually active carriers, that is, the trypanosomes pass through part of their life cycle within their bodies and are not merely transferred mechanically by them as typhoid fever germs are spread by house flies which are passive carriers.

**The genus *Leishmania*.** — The leishmanias are probably transmitted from man to man by sand flies. Kala-azar, a disease widely distributed in Asia, is due to *Leishmania donovani* (Fig. 36, c), a species that attacks especially the endotheial cells and macro-

phages. Also localized in the Far and Near East is *L. tropica*, the organism of oriental sore or cutaneous leishmaniosis. One attack by this species gives immunity to further infection. The type of cutaneous leishmaniosis that occurs in South and Central America is due to *L. braziliensis*, a species that resembles *L. tropica* morphologically but differs from it in its serological reactions.

The genus *Crithidia* is parasitic in arthropods and other invertebrates. A species that may easily be obtained for study is *C. gerridis* (Fig. 36, *f*) from the intestine of water striders of the genus *Gerris*.

The genus *Herpetomonas* also lives in invertebrates. The species that can most readily be secured for examination is *H. muscarum* (Fig. 36, *d*) which lives in the intestine of the common house fly and other flies.

The genus *Phytomonas* (Fig. 36, *e*) is of peculiar interest because it occurs in the latex of plants, such as milkweeds and euphorbias, and is transmitted by hemipterous insects.

**Order POLYMASTIGIDA.** — These are minute flagellates with from three to eight flagella that live mostly in the digestive tract of animals. One or more nuclei are present and in some species a cytostome. Most of the intestinal flagellates of man belong to this order.

**Intestinal flagellates of man.** — There are three common and several rare genera included in this group. *Giardia lamblia* (Fig. 37, *e*) lives in the duodenum where it maintains itself against the force of peristalsis by clinging to the intestinal wall by means of its sucking disk. It multiplies by binary fission and forms cysts which pass out of the body in the feces and are infective to other human beings whose food or drink may become contaminated by them. *Giardias* occur in many other vertebrates and can best be obtained for study from the duodenum of laboratory rats and frog tadpoles. Dogs, cats, mice, rabbits, guinea-pigs, herons, and many other animals are parasitized by their own peculiar species of *giardias*.

*Trichomonads* live in the mouth, large intestine, and vagina and a large percentage of the general population is infected by them. It is not certain that more than one species exist in man but they have been given different specific names. Thus the mouth form is known as *Trichomonas buccalis*; that in the intestine,



*T. hominis* (Fig. 37, a); and the vaginal form, *T. vaginalis*. No cysts are formed by trichomonads hence they must be transmitted in the active, trophozoite stage. Trichomonads are abundant in lower animals. The best way to secure them for study is to examine in

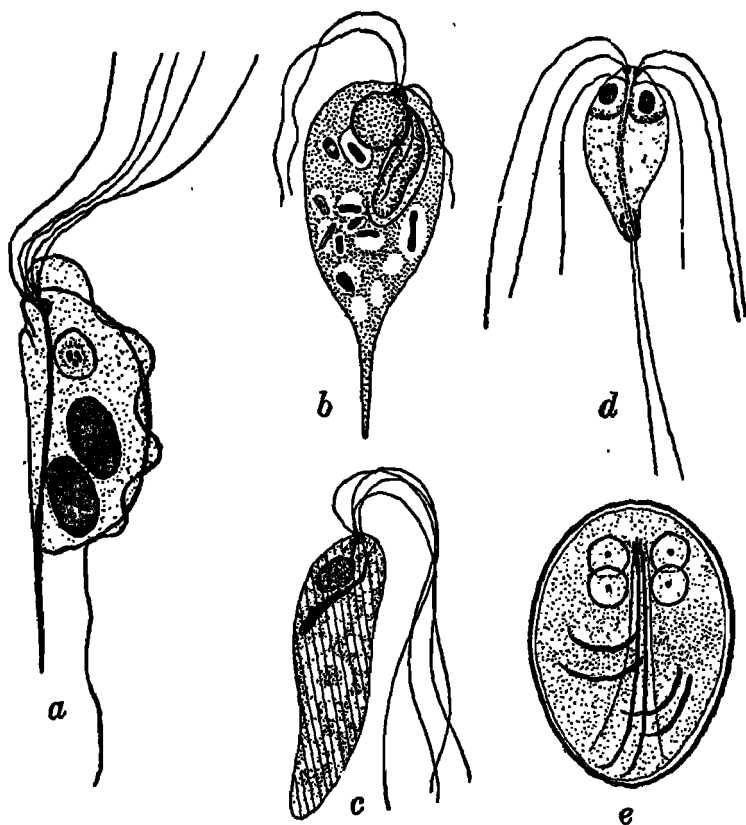


FIG. 37. — Intestinal flagellates. a, *Trichomonas hominis*, from man. b, *Chilomastix mesnili*, from man. c, *Polymastix bufonis*, from the toad. d, *Hexamita salmonis*, from the salmon. e, *Giardia lamblia*, cyst, from man. (After various authors.)

0.7 per cent NaCl solution material from the rectum of the frog or cecum of laboratory rats.

One species of *Chilomastix*, *C. mesnili* (Fig. 37, b), lives in the large intestine of man. Other species occur in rats, rabbits, guinea-pigs, and other common animals. It has not been determined with certainty that giardias, trichomonads, and *Chilomastix* are patho-

genic although many physicians believe them to be the causative agents of flagellate diarrhea.

Many genera belonging to the order PROTOMONADIDA live in lower animals that do not occur in man. Among these are *Hexamita* (Fig. 37, *d*), a genus with six anterior and two posterior flagella, with species living in the small intestine of laboratory rats, of frogs, and toads and other animals, and in stagnant water; *Mono-*

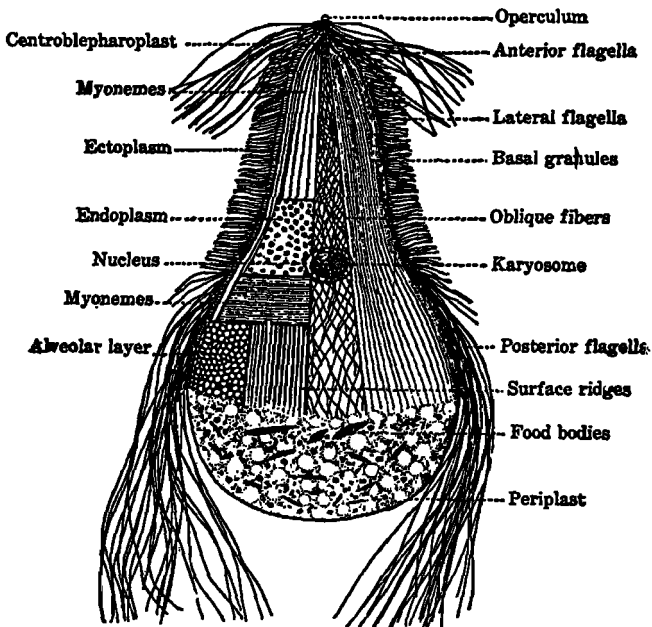


FIG. 38. — HYPERMASTIGIDA. *Trichonympha campanula*. Sections of the body show the structures found at different levels. Surface ridges form the outer layer with their rows of flagella; beneath are successively oblique fibers, alveolar layer and transverse myonemes. In the endoplasm are longitudinal myonemes. (From Kofoed and Swezy.)

*cercomonas*, with a species, *M. bufonis*, which occurs in frogs and toads; and *Polymastix*, with a species, *P. melolonthæ*, in the cockchafer and another, *P. bufonis* (Fig. 37, *c*) in frogs and toads. Besides these a number of genera live in the intestine of termites.

**Order HYPERMASTIGIDA.** — This order includes a number of peculiar flagellates that live in the gut of certain insects and possess some very complex structures. All of the forms bear a large number

of flagella which may be arranged in bunches or may be distributed over the entire body.

**Intestinal flagellates of termites.** — The flagellate inhabitants of the intestine of termites are of special interest because of the number of species, the number of individuals in a single termite, their complexity, the large number of flagella possessed by many of them, and the symbiotic relations between some of them and their hosts. Species from at least eleven families and forty genera of flagellates have been reported from termites. A species that well illustrates the enormous development of flagella and the complexity of the body is *Trichonympha campanula* (Fig. 38). An excellent example of symbiotic relations is furnished by certain of these flagellates and their hosts. The flagellates render the cellulose (in wood) eaten by termites digestible by the insects; without the aid of the flagellates the wood eaten is not digested and the termites

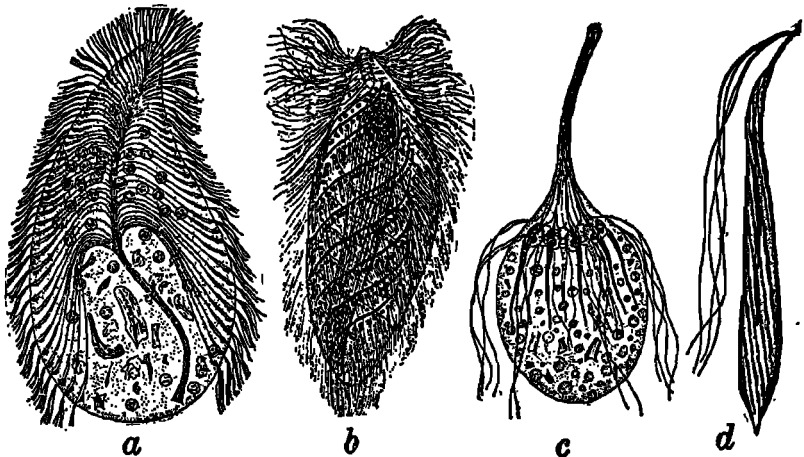


FIG. 39. — Intestinal flagellates of termites. a, *Sunderella tabogæ*, from *Lobitermes longicollis*. b, *Spirotrichonympha flagellata*, from *Reticulitermes lucifugus*. c, *Proboscidiella kofoidi*, from *Cryptotermes dudleyi*. d, *Streblomastix striz*, from *Termopsis laticeps*. (a, c, d, after Kirby; b, after Grassi.)

starve to death. Some of the characteristics of these termite protozoa are illustrated in figure 39.

The genus *Lophomonas* contains species that are common in the intestine of cockroaches. *L. blattarum* has a pyriform body and bears a tuft of flagella at the anterior end. *L. striata* is spindle-shaped and is characterized by rod-like bodies obliquely arranged at the periphery of the body.

## 3. CLASS III. SPOROZOA

## (1) MONOCYSTIS

*Monocystis* is selected as a type of the class SPOROZOA because it illustrates many of the characteristics of this group and is easily

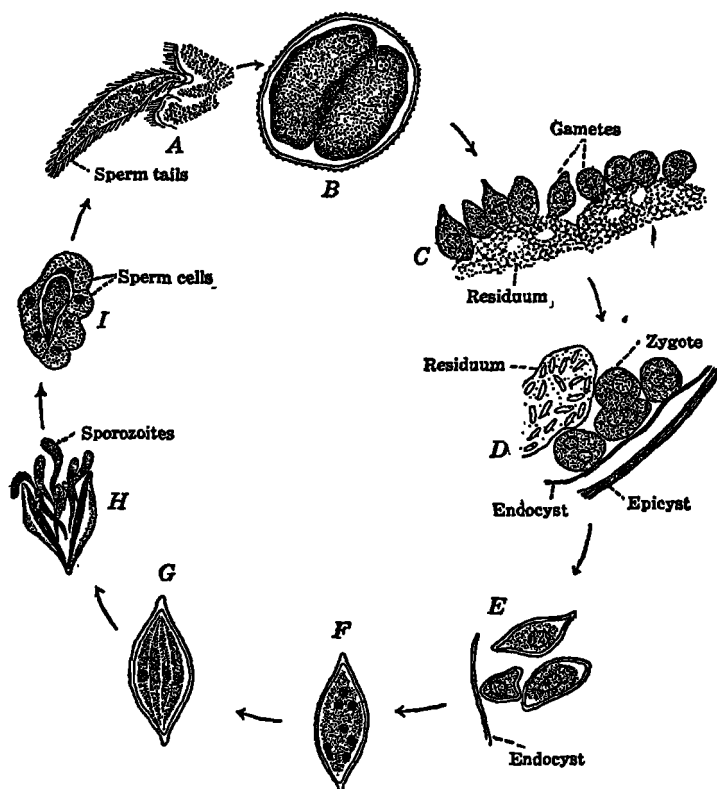


FIG. 40. — GREGARINIDA. *Monocystis*, parasitic in the seminal vesicle of the earthworm. A, a mature individual attached to the sperm-funnel of the earthworm. B, two mature individuals joined side by side. C, gametes formed within the cyst. D, conjugation of gametes to form zygotes. E, zygotes that have become spores. F, a single spore containing eight nuclei. G, a fully developed spore containing eight sporozoites. H, the eight sporozoites escaping from the sporocyst. I, young trophozoite among sperm-mother cells. (After various authors.)

obtained for study. It is a parasite in the seminal vesicles of the common earthworm. A living earthworm should be pinned down and a slit made in the body wall from about the tenth to the

fifteenth segments. The whitish bodies that extrude are the seminal vesicles; parts of these should be pinched off with a forceps and stirred up in a drop of 0.7 per cent NaCl solution on a slide and covered. The stages that are usually present are the trophozoite (Fig. 40, *A*), cysts containing two specimens (*B*), or gametes and spores in various phases of development (*C*, *D*, *E*), and isolated spores (*F*, *G*).

The life cycle of *Monocystis* is briefly as follows. The animals are in some unknown way transferred from one earthworm to another as spores (Fig. 40, *G*), each containing eight elongated bodies called sporozoites (*H*). Each sporozoite penetrates a bundle of sperm mother cells (*I*) of the earthworm, and is then termed a trophozoite. Here it lives at the expense of the cells among which it lies. The spermatozoa of the earthworm which are deprived of nourishment by the parasite, slowly shrivel up finally becoming tiny filaments on the surface of the trophozoite (*A*).

When this stage is reached, two trophozoites come together (*B*) and are surrounded by a common two-layered cyst wall (*D*). Each then divides, producing a number of small cells called gametes (*C*). The gametes unite in pairs (*D*) to form zygotes. It is probable that the gametes produced by one of the trophozoites do not fuse with each other, but with gametes produced by the other trophozoite enclosed in the cyst. Each zygote becomes lemon-shaped, and secretes a thin hard wall about itself. It is now known as a sporoblast (*E*). The nucleus of the sporoblast divides successively into two, four, and finally eight daughter nuclei (*F*); each of these, together with a portion of the cytoplasm, becomes a sporozoite (*G*, *H*).

## (2) PLASMODIUM VIVAX

One of the best known of all the SPOROZOA is *Plasmodium vivax*, which causes tertian malarial fever. This minute animal was discovered in 1880 in the blood of malaria patients by a French military doctor, Laveran. It is transmitted from man to man by the bite of certain species of diseased mosquitoes belonging to the genus *Anopheles*. The two most common genera of mosquitoes are *Culex* and *Anopheles*. One of the easiest methods of distinguishing one from the other is by observing their position when at rest. It will be found that the harmless *Culex* holds its abdomen approximately parallel to the surface on which it alights, whereas the abdomen of *Anopheles* is held at an angle.

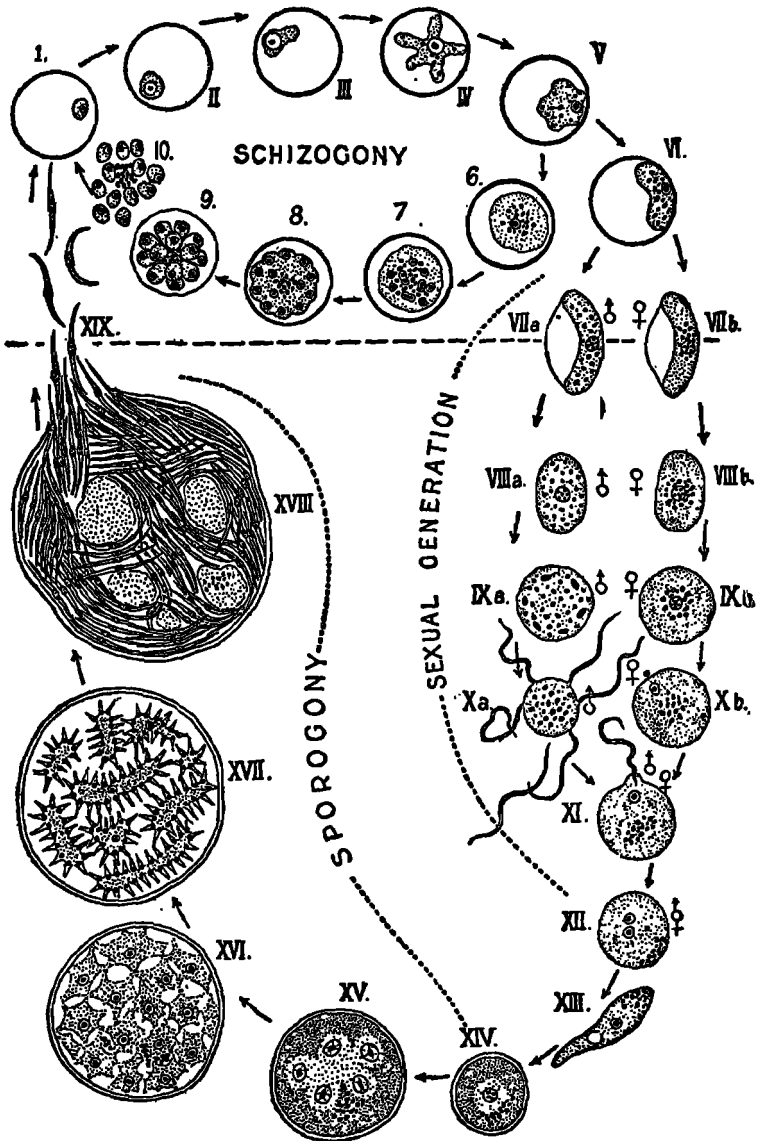


FIG. 41. — *Plasmodium*-of man. Diagram illustrating the life history of the malarial fever parasite. The stages shown above the line of dashes are passed through in the blood of a human being; those below the line, in the body of an *Anopheles* mosquito. For explanations of the stages, see pages 56-57. (From Minchin after various authors.)

There are three well-known types of malaria; these may be recognized by the intervals between successive chills. (1) Tertian fever, caused by *Plasmodium vivax*, is characterized by an attack every forty-eight hours; (2) quartan fever, caused by *Plasmodium malarix*, with an attack every seventy-two hours, and (3) estivo-autumnal or subtertian fever, caused by *Plasmodium falciparum*, produces attacks daily, or more or less constant fever. The life histories of these three species of *Plasmodium* differ very slightly one from another.

Malarial fever is transmitted by diseased female mosquitoes only. The mouth parts of these insects are adapted for piercing. When they have been thrust into the skin of the victim, a little saliva is forced into the wound. This saliva contains a weak poison, which is supposed to prevent the coagulation of the blood and, thus, the clogging of the puncture. Blood is sucked up by the mouth parts into the alimentary canal of the mosquito; this process occupies from two to three and a half minutes. With the saliva a number of parasites, which were stored in the salivary glands of the insect, find their way into the wound. These are known as *sporozoites* (Fig. 41, XIX). Each sporozoite penetrates a red blood corpuscle, becoming an amoeba-like *trophozoite*, which feeds and grows at the expense of the protoplasm of the red blood corpuscle (I-V). The trophozoite reaches its full size in about fifty hours and is then known as a *schizont*; this undergoes a type of multiple division, thus producing from fifteen to twenty-four daughter cells which are called *merozoites* (6-10). The merozoites are liberated into the blood stream in about eight hours and immediately attack fresh red blood corpuscles. Some of the merozoites develop into schizonts, but others become sexual cells called *gametocytes* (VI).

When a mosquito bites a malaria patient it sucks up blood containing gametocytes. If the mosquito is of the genus *Culex* or of some genus other than *Anopheles*, the parasites are, in the course of time, destroyed in its stomach; but if the mosquito is a female belonging to the proper species of *Anopheles*, development is completed. The female gametocyte produces a mature *macrogamete* (VII, b-X, b), and within the male gametocyte six to eight flagella-like bodies develop which are *microgametes* comparable to spermatozoa (VII, a-X, a). Fertilization then ensues (XI) and the zygote (XII) thus formed changes into a motile, worm-like *ookinete* (XIII) which enters the wall of the mosquito's stomach. Here it

rounds up into an *oocyst* (XIV) which grows at the expense of the surrounding tissue, and after six or seven days undergoes *sporulation* during which hundreds of spindle-shaped sporozoites are produced (XV–XVIII). These break out into the body cavity of the mosquito and some of them find their way into its salivary glands; here they remain ready to be injected into the next human being the mosquito bites.

Malaria is probably the most important of all human diseases, since it not only causes thousands of deaths and great suffering to millions of people every year, especially in tropical and subtropical regions, but also prevents the cultivation of vast areas of the most fertile regions on the earth. Fortunately, we know how it is transmitted and can control it by destroying mosquitoes and their larvæ. Also, in quinine, we have a therapeutic agent that destroys the parasites in the human body. Recently a new drug, called plasmochin, has been developed that in some respects is supplementary to quinine.

### (3) OTHER SPOROZOA

The SPOROZOA are all parasitic PROTOZOA which usually pass from one host to another in the spore stage. The spore is generally a seed-like body with a covering called the *sporocyst* (Fig. 40, *F*, *G*). In species whose spores are subjected to air, water, or other agents in their passage from one host to another, these bodies are very resistant, but in other species which are propagated from one host to another directly, either by being inoculated into the new host by a blood-sucking animal or by being eaten by the new host, the spores do not always have such a resistant covering (Fig. 41).

SPOROZOA are among the most widely distributed of all parasitic animals; members of almost every large group of animals in the animal kingdom are parasitized by one or more species. Infection is very common among the vertebrates, arthropods, mollusks, and worms, and less common among echinoderms, coelenterates, and PROTOZOA. Comparatively few species are lethal and only a small number seem to be very harmful to their hosts.

The life cycles of the SPOROZOA are often very complicated. Frequently there is an alternation of hosts, certain stages being passed in a vertebrate and other stages in an invertebrate which serves as a transmitting agent from one vertebrate host to another. Two types of reproduction are characteristic of the life cycles of



most species, (1) multiplicative reproduction or *schizogony* during which many organisms are formed in a single host, and (2) propagative reproduction involving sexual processes and ending in the formation of spores which are usually transferred to another host.

As compared with the other three classes of PROTOZOA, the SPOROZOA are greatly modified by their parasitic existence. These modifications are represented by the absence of locomotor organs, a mouth, anal opening, excretory pore, and vacuoles. There is usually a single nucleus present. Nutrition is by absorption. Many organs of the host may be parasitized, especially the alimentary tract, kidneys, blood, muscle, and connective tissues. When the parasites live inside of cells they are said to be *cytozoic*; when among the cells, *histozoic*; and when in cavities, *cælozoic*.

**Classification of the Sporozoa.** — The groups that are brought together in the class SPOROZOA have certain characteristics in common but are not necessarily closely related. They are combined in one class largely for the sake of convenience. It seems best to separate them into three subclasses and to divide these into orders.

The subclass TELOSPORIDIA contains three orders: (1) GREGARINIDA, (2) COCCIDIA, and (3) HÆMOSPORIDIA. The members of these orders produce spores that have neither polar capsule nor polar filament and that are produced at the termination of the life of the trophozoite.

**Order GREGARINIDA.** — The gregarines are common parasites of insects, especially in the digestive tract and body cavity, and less common in other groups of vertebrates and invertebrates. They are, at first, intracellular but later often become free in cavities of the body. Here they sometimes grow to a comparatively enormous size. *Monocystis* has already been described (Fig. 40). Another type that is easily obtained for study is *Gregarina* (Fig. 42, b) which occurs in the intestine of grasshoppers, cockroaches, and meal-worms. The sporozoites penetrate the epithelial cells of the intestinal wall and the trophozoites which develop from them are at first intracellular; later the trophozoites break out of the epithelial cell to which they are attached for a time by the head or *epimerite*; this, the *cephalont* stage, consists of two parts, the posterior *deutomerite* which contains the nucleus, and an anterior *protomerite* and *epimerite* (Fig. 42, a). When the cephalont becomes detached from the cell it loses its epimerite and is then

known as a *sporont*. The sporonts within the intestine unite end to end, a condition known as *syzygy* (Fig. 42, *b*). Two sporonts conjugate and surround themselves with a wall thus forming a cyst; they are gametocytes, each of which produces a large number of gametes. The gametes copulate in pairs, thus becoming zygotes, and secrete sporocysts and hence are spores. Within each spore eight sporozoites are produced. The sporozoites that are liber-

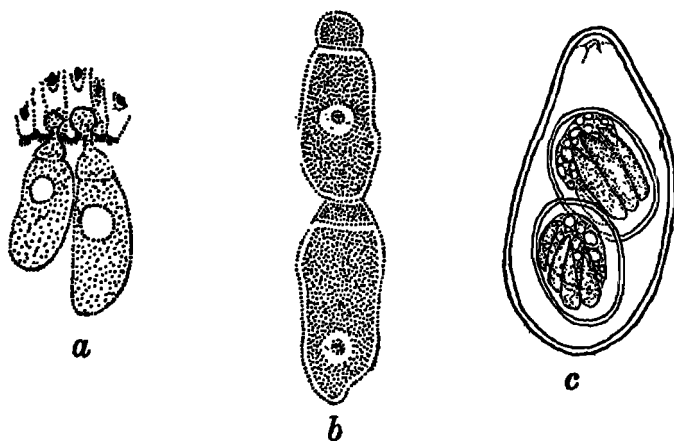


FIG. 42. — TELOSPORIDIA. *a*, GREGARINIDA. *Leidyana erratica* attached to intestinal cells of cricket. *b*, GREGARINIDA. *Gregarina blattarum* of the cockroach; two animals attached end to end in syzygy. *c*, COCCIDIA. *Isospora hominis* of man; oocyst containing two spores, each with four sporozoites. (After various authors.)

ated in the intestine of the hosts that have ingested the spores bring about new infections.

**Order COCCIDIA.** — The COCCIDIA are SPOROZOA whose life cycle includes both schizogony and sporogony and is passed in a single host. They are parasitic in vertebrates, myriapods, mollusks, insects, annelids, and flatworms. The life cycle of a typical species, *Isospora felis* of the cat, is illustrated in figure 43.

The sporozoites that escape from the spores in the intestine of the host (30) penetrate epithelial cells of the intestinal wall (1) and become trophozoites (2); each trophozoite is a schizont which produces a number of daughter merozoites asexually (3-8); this multiplicative process is known as schizogony. The merozoites may enter other epithelial cells (8-1) becoming trophozoites and pass through another period of asexual reproduction, or, after the

penetration of epithelial cells, may produce merozoites which are gametocytes; these penetrate other epithelial cells (9) where they develop into macrogametocytes (19) or microgametocytes (11). Each merozoite produces either one large macrogamete (22) or a large number of microgametes (18). One microgamete copulates with each macrogamete (23), a process that may be considered fertilization, thus producing a zygote. A wall forms about the zygote and the body is then known as an oocyst (24). The protoplasm within divides to form two sporoblasts (28) each of which forms a sporocyst about itself thus becoming a spore (29). Within each spore four sporozoites develop (29).

**Coccidia in man.** — The single species of coccidium, *Isospora hominis*, that lives in man is known only in the oocyst stage (Fig. 42, c). Its life cycle is probably similar to that of *Isospora felis*. Human beings become infected by swallowing oocysts with which their food or drink has become contaminated. The infection is characterized by diarrhea which lasts about two weeks. This species seems to be rare since only a few cases have been recorded.

**Coccidia in lower animals.** — The COCCIDIA most easily obtained for study are those in the rabbit, *Eimeria stiedæ*. Oocysts of this species may be found in the feces of a large proportion of these animals. They are in an unsegmented stage when passed but segmentation may be observed if the material is placed in a 5 per cent aqueous solution of potassium bichromate to inhibit the growth of bacteria. Segmentation into sporoblasts and the formation of sporozoites takes place in about three days.

Other species of *Eimeria* occur in various species of mammals, birds, reptiles, amphibians, and fish. All of these are pathogenic if their life cycles are similar to that of *E. stiedæ* in the rabbit, but most of them do not injure the host very severely. *E. stiedæ* frequently brings about the death of rabbits, however, and *E. zürnii* is the cause of diarrhea in cattle, especially in Switzerland, Sweden, and Denmark. The *Eimeria* of birds, *E. tenella*, is likewise lethal under certain conditions, especially when epidemics occur among young chickens.

Coccidia of the genus *Isospora* also occur in vertebrates of all classes. Cats and dogs are commonly infected with *I. felis* and *I. rivolta*. Other species occur in birds and cold-blooded vertebrates.

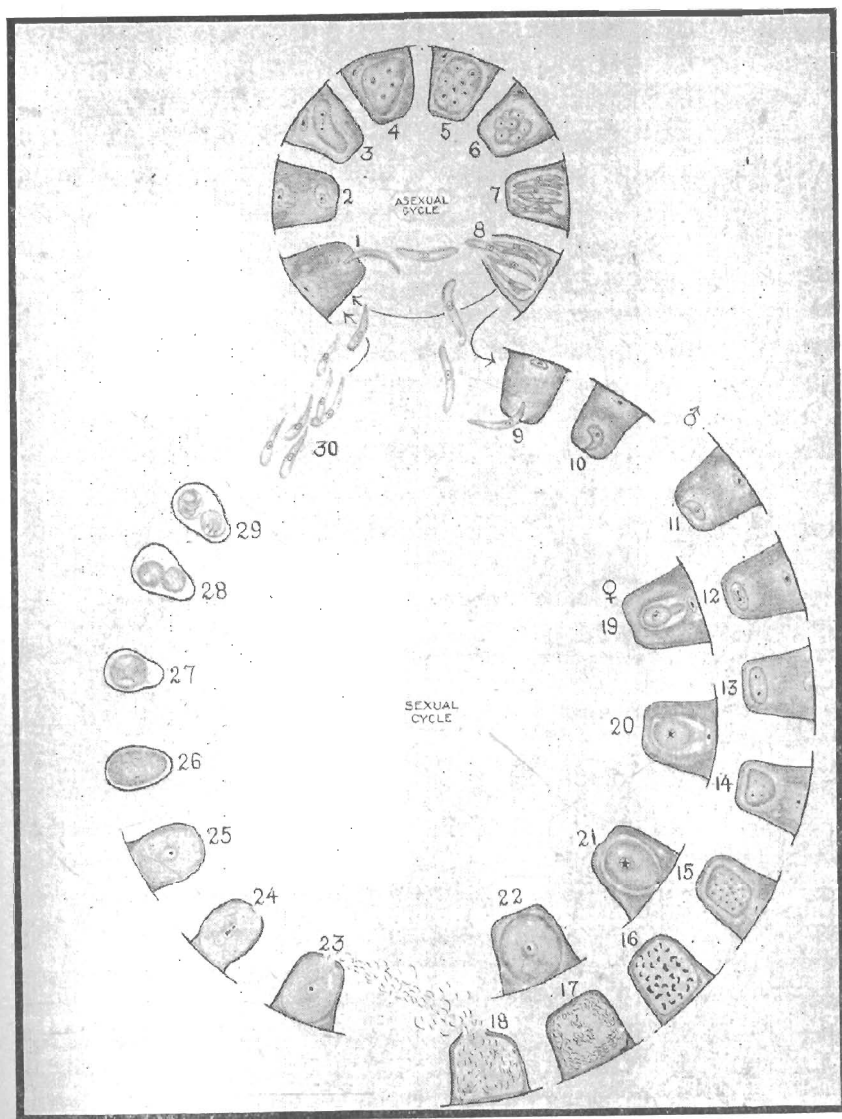


FIG. 43. — COCCIDIA. *Isospora felis*, life cycle; a coccidian that lives in cats. Stages 26, 27, 28, and 29 are oocysts which pass out of the body with the faeces; in each oocyst two sporoblasts are formed (28) and in each sporoblast four sporozoites (29). When ingested by a susceptible animal the sporozoites escape from the oocyst (30), enter epithelial cells (1) where they undergo schizogony (2-8). The merozoites produced may repeat the asexual cycle (8 to 1 to 8) or initiate the sexual cycle (9-25). In the latter, female cells (♀) or macrogametes (19-22) and male cells (♂) or microgametes (11-18) develop. Fertilization (23) is followed by the formation of the oocyst (24-26). (After Andrews.)

**Order HÆMOSPORIDIA.** — The HÆMOSPORIDIA, as the name implies, are SPOROZOA that live in the blood. They penetrate the blood cells of vertebrates where they pass through schizogony and go through part of their life cycle in invertebrate hosts where sporogony occurs. The most important species are the malarial parasites of man. Representatives of a number of genera may be obtained from common lower animals, for example, *Hæmoproteus* from birds; *Cytamæba* and hæmogregarines from frogs; piroplasmas and anaplasmas from cattle suffering from Texas fever; and *Plasmodium* from birds. In every case preparations are made by securing a drop of fresh blood, spreading it on a slide where it is allowed to dry, and then staining it by a Romanowsky method.

*Hæmoproteus* (Fig. 44, a) is a genus common in birds, turtles, snakes, and lizards. The best-known species is *H. columbæ*, a parasite of the common pigeon that has been reported from vari-

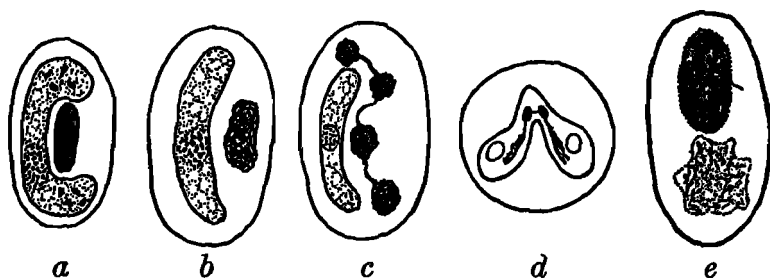


FIG. 44. — HÆMOSPORIDIA. a, *Hæmoproteus* in the red blood corpuscle of a bird. b, *Lankesterella* in the red blood corpuscle of a frog. c, *Karyolysus* in the red blood corpuscle of a frog. d, *Babesia canis* in the red blood corpuscle of a dog. e, *Cytamæba* in the red blood corpuscle of a frog. (a; b, c, e after Hegner; d, after Nuttall.)

ous parts of the world. The life cycle of this species includes asexual reproduction in the endothelial cells of the blood vessels of the pigeon's lungs and other organs, and the development of male and female gametocytes. The transmitting agent in which sporozoites are formed is a hippoboscid fly, *Lynchia maura*. Within the red cells the organism grows partly around the red-cell nucleus in the form of a halter, hence the term halteridium often applied to members of this genus.

Hæmogregarines of the genera *Lankesterella* and *Karyolysus* may be encountered in the blood of frogs. *Lankesterella* (Fig. 44, b) pushes the nucleus of the frog's red corpuscle in which it lives to

one side. *Karyolysus* (Fig. 44, c) causes the nucleus of the parasitized red corpuscle to break up into several pieces. The life cycle of the hæmogregarine in the rat, *Hepatozoon muris*, is well known; the transmitting agent is a mite which feeds on the blood of the rat and may be eaten by another rat which then becomes infected.

*Cytamæba bacterifera* (Fig. 44, e) is a peculiar organism that occurs in the red blood corpuscles of frogs. It is amœboid in character and throws out pseudopodia when alive. Within it are many rod-shaped, bacillus-like bodies that are actively moving.

Piroplasmas of the genus *Babesia* occur in cattle, sheep, goats, horses, dogs, and various game animals. *B. canis* (Fig. 44, d) of the dog is the best known. *B. bigemina* causes Texas fever in cattle and members of the genus *Anaplasma* appear as minute spherical bodies in the red blood corpuscles of cattle suffering from a disease called anaplasmosis. Very little is known about this group of organisms.

Malarial parasites of the genus *Plasmodium* occur in lower animals as well as in man. They have been recorded especially from birds, bats, squirrels, and lizards. The species in birds are of particular interest because they were used by Ross in working out the sexual cycle of malarial parasites in mosquitoes. They are also of great value for purposes of teaching and investigation since they can be transmitted easily from sparrows to captive canaries by blood inoculation, and when the latter are once infected they appear to remain infected throughout their lives. The method of procedure is to prick a vein in the leg and suck up a drop of blood into a syringe containing normal saline solution. This is then injected into the breast muscle or peritoneal cavity of a fresh bird. The average length of the prepatent period is about five days. The period of rise in the number of parasites is also about five days when from ten to 5000 parasites per 10,000 red cells are present. Then a rapid fall in the number of parasites occurs and no more can be found in the blood except after long search. That the birds remain infected is evident from the fact that they suffer relapses, much as human beings do, and also by the fact that blood from the birds is infective to fresh birds. Bird malaria is of value for the study of therapeutic agents. The drug known as plasmochin was first found to be effective against the plasmodia of birds and later of man.

The subclass CNIDOSPORIDIA contains SPOROZOA that produce

spores in each of which are one to four polar capsules and in each polar capsule a coiled polar filament. The two principal orders are the MYXOSPORIDIA and MICROSPORIDIA.

**Order MYXOSPORIDIA.** — The MYXOSPORIDIA (Fig. 45, *a, b*) are principally parasites of fish. Of the 237 known species, 223 are fish parasites, 8 inhabit AMPHIBIA, 4 reptiles, 1 insects, and 1 annelids (Kudo). The life cycle is comparatively simple, since there is no intermediate host. The principal organs of the host invaded by the parasite are the gall-bladder, gills, kidney, urinary bladder, muscle, integument, connective tissue, spleen, and ovary. The spores are complicated structures (Fig. 45, *b*). When swallowed by a new host, the polar filaments are extruded and

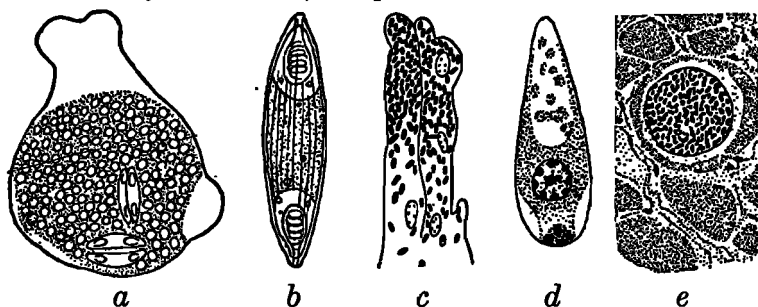


FIG. 45. — CNIDOSPORIDIA and ACNIDOSPORIDIA. *a*, MYXOSPORIDIA; *Myxidium lieberkuhni*, vegetative stage, from pike. *b*, MYXOSPORIDIA; *Myxidium lieberkuhni*, spore, from pike. *c*, MICROSPORIDIA; *Nosema apis*, spores in cells of stomach of honeybee. *d*, MICROSPORIDIA; *Thelohania magna*, young spore from larva of mosquito. *e*, SARCOSPORIDIA; Spores in muscle fibers of man. (After various authors.)

probably fix the spore to the intestinal wall. Then begins a life cycle of too great complexity to be described here. Frequently infections are severe and bring about the death of the host.

**Order MICROSPORIDIA.** — The MICROSPORIDIA (Fig. 45, *c, d*) are characterized by the presence of spores that are extremely small and possess usually only one polar capsule. Kudo (1924) records 178 species living in 222 different host species of which 149 are arthropods; the rest belong to other groups of invertebrates and to the cold-blooded vertebrates. Among the invertebrate hosts are included three species of SPOROZOA and one ciliate. Certain of the MICROSPORIDIA are of great economic importance because they bring about the death of animals of value to man. For example, the species *Nosema bombycis* causes a chronic disease in

silkworms known as pebrine. This species is generally distributed throughout the tissues of the host, including the eggs developing in the ovary. These eggs are deposited by the silkworm moth and the larvæ that hatch from them are thus infected by the so-called "hereditary" transmission. Pasteur was able to control silkworm disease, which once threatened to destroy the silk industry of France, by eliminating infected eggs which he was able to recognize with the aid of a microscope. Another important species economically is *Nosema apis* (Fig. 45, c) which causes nosema disease in honeybees. Infection is brought about by the ingestion of spores and is limited to the digestive tract. Other species of MICROSPORIDIA are to a certain degree beneficial because they attack harmful insects, for example, the larvæ of several species of anopheline mosquitoes that are carriers of human malaria may be infected.

The subclass ACNIDOSPORIDIA contains two orders of doubtful position, the SARCOSPORIDIA and the HAPLOSPORIDIA.

**Order SARCOSPORIDIA.** — The spores of the SARCOSPORIDIA do not contain polar capsules. SARCOSPORIDIA are parasites of vertebrates, being especially common in sheep, cattle, and horses. They occur in reptiles and birds as well as mammals. The life cycle of the sarcosporidium of rats and mice, *Sarcocystis muris*, is the best known. Spores ingested by mice hatch in the intestine, and liberate amœbulæ that penetrate the cells of the intestinal epithelium; here the trophozoites grow and multiply by schizogony. Apparently the merozoites migrate to the muscles where they become located in the fibers; here growth results in a multinucleate plasmodium which divides by plasmotomy. In the course of time the masses of parasites form long, slender, cylindrical bodies with pointed ends, known as "Miescher's tubes" within which immense numbers of sickle-shaped spores are formed. Very little is known regarding the method of transmission of SARCO-SPORIDIA.

Half a dozen cases of sarcosporidiosis have been reported from man, the organisms being found in the muscle usually at autopsy (Fig. 45, e). In most cases no serious results are brought about by the infection, although *S. muris*, which spreads throughout the entire body, brings about death in mice, and death sometimes also occurs in sheep as a result of heavy infections. A toxic substance called sarcocystin, which is lethal to rabbits, has been



reported from SARCOSPORIDIA. The death of infected hosts may be due to this toxin.

**Order HAPLOSPORIDIA.** — The HAPLOSPORIDIA are parasites of lower vertebrates and invertebrates. The genus *Haplosporidium* occurs in marine and fresh-water annelids and molluscs. *Ichthyosporidium* is parasitic in fish. *Bertramia* parasitizes aquatic worms and rotifers.

#### 4. CLASS IV. INFUSORIA

##### (1) PARAMÆCIUM

*Paramæcium* lives in fresh-water ponds and streams, and is very easily obtained. Cultures prepared for *Amœba* will in most cases sooner or later contain a host of *Paramœcia*.

**General morphology** (Fig. 46). — If a drop of water containing *Paramœcia* is placed on a slide, the animals may be seen with the naked eye moving rapidly from place to place. Under the microscope they appear cigar-shaped (Fig. 46). A closer view reveals a depression extending from the end directed forward in swimming, obliquely backward and toward the right, ending just posterior to the middle of the animal. This is the *oral groove*. The *cytostome* is situated near the end of the oral groove. It opens into a funnel-shaped depression called the *cytopharynx* or *gullet*, which passes obliquely downward and posteriorly into the *endosarc*. The oral groove gives the animal an unsymmetrical appearance. Since *Paramœcium* swims with the slender but blunt end foremost, we are able to distinguish this as the *anterior end*. The opposite end, which is thicker but more pointed, represents the *posterior end*, while the side containing the oral groove may be designated as *oral* or *ventral*, the opposite side *aboral* or *dorsal*. The motile organs are fine thread-like *cilia* regularly arranged over the surface. Two layers of cytoplasm are visible, as in *Amœba*, an outer comparatively thin clear area, the *ectosarc* and a central granular mass, the *endosarc*. Besides these a distinct *pellicle* or *periplast* is present outside of the *ectosarc*. Lying in the ectoplasm are a great number of minute sacs, the *trichocysts*, which discharge long threads to the exterior when properly stimulated. One large *contractile vacuole* is situated near either end of the body, close to the dorsal surface, while a variable number of *food vacuoles* may usually be seen. The *nuclei* are two in number, a large *macro*

*nucleus* and a smaller *micronucleus*; these are suspended in the ectoplasm near the mouth opening. The *anal spot* can be observed only when solid particles are discharged. It is situated just behind the posterior end of the oral groove.

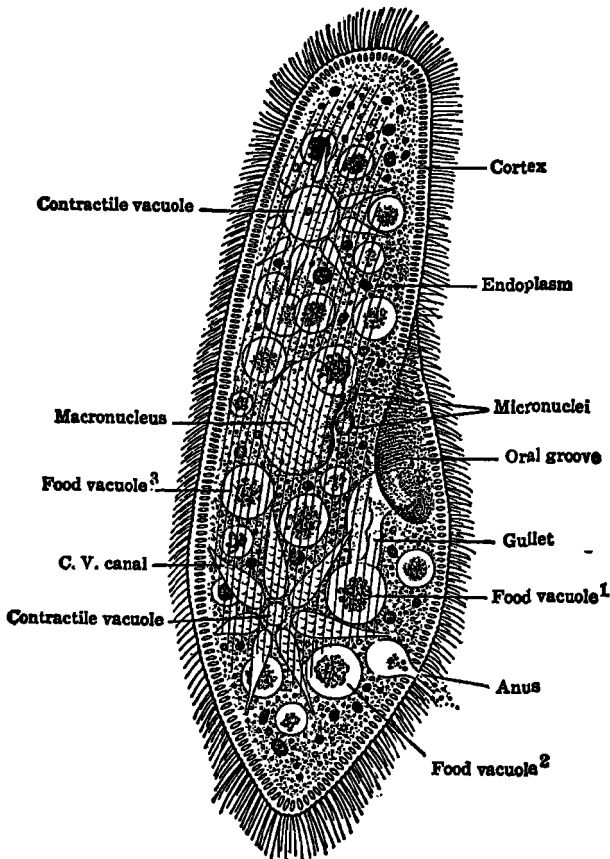


FIG. 46. — *Paramecium aurelia* viewed from the side. This has two micronuclei. (From Newman after Pfuertscheller wall chart.)

**Cytology.** — The *endoplasm* of *Paramecium* occupies the central part of the body. It is supposed to be alveolar in structure. Most of the larger granules contained within it are shown by micro-chemical reactions to be reserve food particles; they flow from place to place, indicating that the protoplasm is of a fluid nature. The *ectoplasm* does not contain any of the large granules char-

acteristic of the endoplasm, since its density prevents their entrance. In this respect the two kinds of cytoplasm resemble the ectoplasm and endoplasm of *Amæba*. If a drop or two of 35 per cent alcohol is added to a drop of water containing *Paramæcia*, the pellicle will be raised in some specimens in the form of a blister. Under the higher powers of the microscope the pellicle is then seen to be made up of a great number of hexagonal areas produced by *striations* on the surface (Fig. 50). These striations are really very fine grooves which cross one another obliquely.

The distribution of the motile organs, the *cilia* (Fig. 47), corresponds to the arrangement of the striations on the cuticle, since



FIG. 47. — Schematic representation of the beating of a row of cilia. (After Verworn.)

one cilium projects from the center of each hexagonal area (Fig. 50, c). These thread-like structures occur on all parts of the body, those at the posterior end being slightly longer than elsewhere. A cilium may be compared to a very fine pseudopodium which has become a permanent structure. It is an outgrowth of the cell protoplasm, coming from a basal body called a microsome (Fig. 50, d) which appears to arise from the nucleus. A fusion of cilia has occurred within the mouth cavity, producing the *undulating membrane* (Fig. 53). This is attached to the dorsal wall of the mouth, and guides the food particles that are swept within its reach.

Just beneath the cilia, embedded in the cortical layer of the ectoplasm, is a uniform layer of spindle-shaped structures  $\frac{1}{1000}$  mm. in length, lying with their long axes perpendicular to the surface (Fig. 53). These are *trichocysts*. They appear to be cavities in the ectoplasm filled with a semi-liquid homogeneous substance which is very refractive. They arise in the neighborhood of the nucleus. A small amount of osmic or acetic acid, when added to a drop of water containing *Paramæcia*, causes in some cases the discharge of the trichocysts to the exterior through very small canals. This explosion is due to the pressure derived from the contraction of the cortical layer of the ectoplasm. After the explosion, the trichocysts appear as long threads which have been extended to about eight times their former length. Trichocysts are supposed to function as weapons of offense and defense. It is said

that their contents are discharged with considerable force and that they contain a poison strong enough to paralyze any single-celled animal. Evidence that the trichocysts are weapons of defense is furnished when *Paramæcium* encounters another ciliate *Didinium*. If the seizing organ of this protozoon becomes fastened in the *Paramæcium*, a great number of trichocysts near the place of the injury are discharged (Fig. 48). These produce a substance which

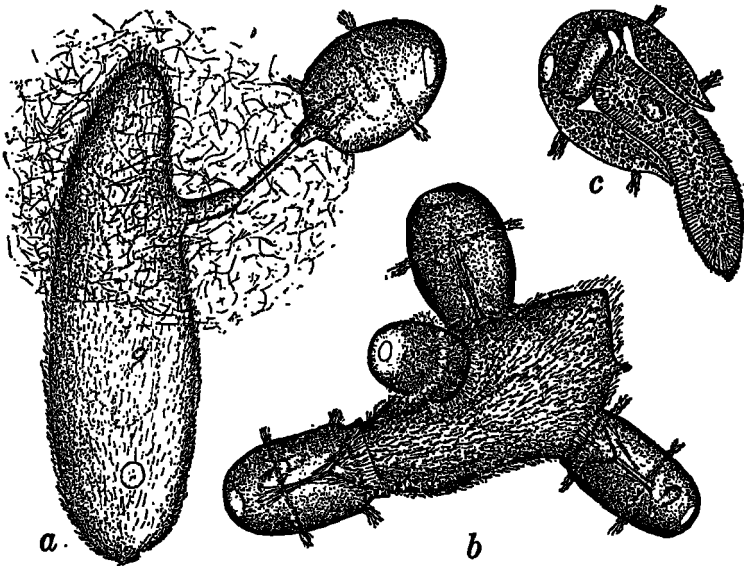


FIG. 48. — *Paramæcium* attacked by the ciliate *Didinium nasutum*. a, *Paramæcium* discharges its trichocysts thus forcing the attacking *Didinium* away. b, Four small didinia attacking a *Paramæcium*. c, Section of a large *Didinium* swallowing a small *Paramæcium*. (After Mast.)

becomes jelly-like on entering the water; this tends to force the two animals apart, and, if the *Paramæcium* is a large one, it frequently succeeds in making its escape.

Two *contractile vacuoles* are present, occupying definite positions, one near either end of the body. They lie between the ectoplasm and the endoplasm, close to the dorsal surface, and communicate with a large portion of the body by means of a system of *radiating canals*, six to ten in number. The vacuoles grow in size by the addition of liquid which is excreted by the protoplasm into the canals and is then poured into them. When the full size is reached,

the walls contract and the contents are discharged to the exterior, probably through a pore. The two vacuoles do not contract at the same time, but alternately, the interval between successive contractions being ten to twenty seconds. The expulsion of the fluid contents of the contractile vacuoles may be seen in the following way. *Paramæcia* should be mounted in water into which has been rubbed up a stick of India or Chinese ink. They then appear white against a black background. Part of the water should be withdrawn from beneath the cover glass, thus slightly compressing them. If now a specimen in profile is found and watched, the discharge produces a bright spot outside in the opaque liquid; this lasts from one

to two seconds, and is then driven off by the cilia (Fig. 49).

In *Paramæcium trichium* the two contractile vacuoles are permanent structures with vesicles that collect and pour fluids into them and with a long convoluted excretory tubule ending in an excretory pore opening on the aboral surface. The duration of the systole is long compared with that

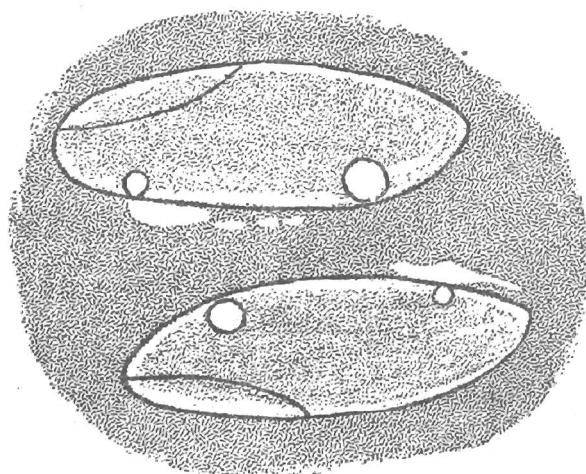


FIG. 49. — *Paramæcium*: discharge of contractile vacuoles. The organisms are represented swimming in a solution of India ink. (After Jennings.)

of the diastole due probably to the presence of the excretory tubule. What has been said of the function of the contractile vacuole in *Amæba* applies as well to that of *Paramæcium*, i.e. it acts as an organ of excretion and respiration, and is probably hydrostatic. Most of the nitrogen secreted by *Paramæcium* is in the form of urea and this substance has been detected in the contractile vacuole. However, the greater part of the excretory matter, including urea, apparently passes by dialysis directly to the exterior through the pellicle. That the primary function of the contractile vacuole is to regulate the water content of the protoplasm is indicated by the correlation between the frequency of pulsation and the rate water is taken in. For example,

most long periods between pulsations, up to six minutes when actively swimming, occur when little water is ingested, and most short periods occur when the animals are at rest.

Certain granules and associated fibrils have been described in *Paramæcium* and considered to constitute a neuromotor apparatus sensory in function and of use in coordinating motion (Figs. 50, 51). Longitudinal ciliary fibrils, transverse commissural fibrils,

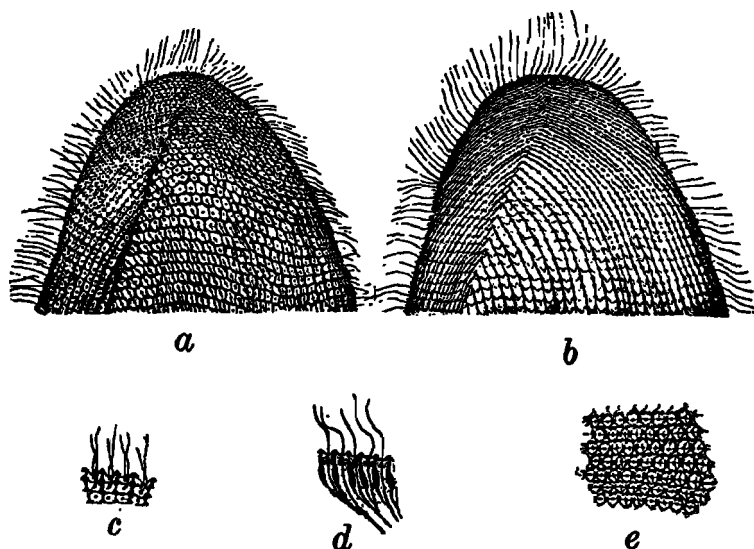


FIG. 50. — *Paramæcium caudatum*. Drawings designed to show the neuromotor apparatus. a, Anterior end showing the hexagonal sculpturing of the pellicle, the supportive preoral suture, the contractile organelles, which are wide and dark on the edges of the hexagons, the longitudinal ciliary fibrils of the neuromotor system, and the basal granules. b, Anterior end showing structures just beneath the pellicle, especially the longitudinal ciliary fibrils and curved commissural neurofibrils running transversely. c, Edge of pellicle showing basal granules in the center and papillae at corners of the "dimples." d, Section through surface layer showing trichocysts and internal neurofibrils arising from base of basal granules. e, External structure of pellicle showing hexagon-shaped "dimples," light papillae at the corners, basal granules, longitudinal ciliary fibrils and transverse commissural fibrils. (After Brown.)

and internal neurofibrils are present connected to the granules at the base of the cilia. These granules are connected near the periphery by the longitudinal ciliary fibrils and transversely by the commissural fibrils. The neurofibrils extend a short distance into

the endoplasm and are perpendicular to the peripheral fibrils; they unite with each other and form a fan-like system. (Brown.)

**Locomotion.** — The only movements of *Paramæcium* that in any way resemble those of *Amæba* are seen when the animal passes

through a space smaller than its shorter diameter; it will then exhibit an elasticity which allows it to squirm through. In a free field *Paramæcium* swims by means of its cilia. "These are usually inclined backward, and their stroke then drives the animal forward. They may at times be directed forward; their stroke then drives the animal backward. The direction of their effective stroke may indeed be varied in many ways, as we shall see later. In addition to its forward or backward movement *Para-*

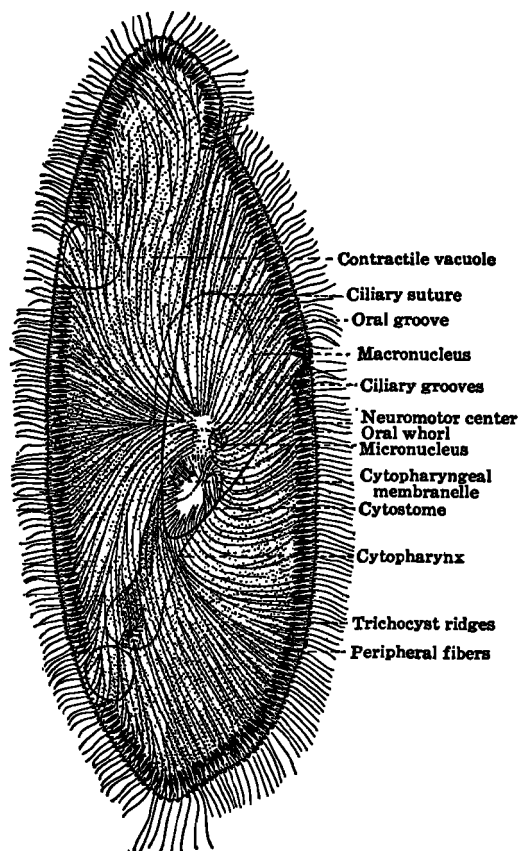


FIG. 51. — *Paramæcium caudatum*. Oral view showing oral whorl of peripheral fibers and the ciliary lines, ciliary suture, and trichocyst ridges. (After Rees.)

rotation is over to the left, both when the animal is swimming forward and when it is swimming backward. The revolution on the long axis is not due to the oblique position of the oral groove, as might be supposed, for if the animal is cut in two, the posterior half, which has no oral groove, continues to revolve.

"The cilia in the oral groove beat more effectively than those

elsewhere. The result is to turn the anterior end continually away from the oral side, just as happens in a boat that is rowed on one side more strongly than on the other. As a result the animal would swim in circles, turning continually toward the aboral side, but for the fact that it rotates on its long axis. Through the rotation the forward movement and the swerving to one side are combined to produce a spiral course. The swerving when the oral side is to the left, is to the right; when the oral side is above, the body swerves downward; when the oral side is to the right, the body swerves to the left, etc. Hence the swerving in any given direction is compensated by an equal swerving in the opposite direction; the resultant is a spiral path having a straight axis" (Fig. 52).

Rotation is thus effective in enabling an unsymmetrical animal to swim in a straight course through a medium which allows deviations to right or left, and up or down. It is well known that a human being cannot keep a straight course when lost in the woods, although he has a chance to err only to the right or left.

**Nutrition.** — The *food* of *Paramæcium* consists principally of bacteria and minute protozoa. The animal does not wait for the food to come within its reach, but by continually swimming from place to place is able to enter regions where favorable food conditions prevail. The cilia also aid in bringing in food particles, since a sort of vortex is formed by their arrangement about the oral groove which directs a steady stream of water toward the mouth.

Figure 53 illustrates the formation of a *food vacuole*. Food particles that are swept into the mouth are carried down into the



FIG. 52. — *Paramæcium*: spiral path. 1, 2, 3, 4, successive positions occupied. The dotted areas with small arrows show the currents of water drawn from in front. (From Jennings.)



cytopharynx by the undulating membrane; they are then moved onward by the cilia lining the cytopharynx and are finally gathered together at the end of the passageway into a vacuole which gradually forms in the endoplasm.

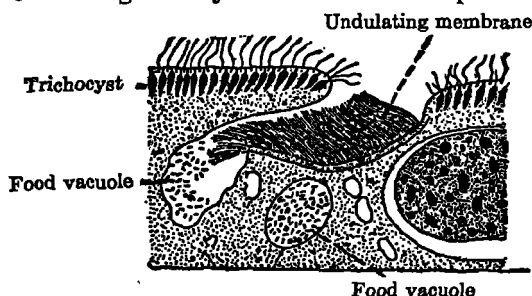


FIG. 53. — *Paramacium*: formation of food vacuole. Section through cytopharynx showing the manner in which bacteria are swept into the food vacuole in process of formation. (After Maier.)

water with food particles suspended within it. As soon as one is separated from the cytopharynx, it is swept away by the rotary streaming movement of the endoplasm known as *cyclosis*. This carries the food vacuole around a definite course which begins just above and behind the cytopharynx, passes backward to the posterior end, then forward near the dorsal surface to the anterior end, and finally downward and along the ventral surface toward the mouth. During this journey digestion takes place.

Unlike *Amœba* a special *anal spot* or *cytopyge* (Fig. 46) is present in *Para-*

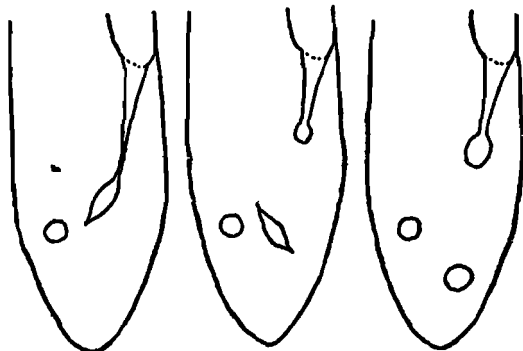


FIG. 54. — *Paramacium caudatum*. Successive stages in the formation of food vacuoles. (After Dunihue.)

*macium* through which indigestible solids are discharged to the outside. This opens on the ventral surface just behind the mouth. It can be seen only when material is cast out. It is not yet known whether the anal spot is a permanent orifice whose lips are

so tightly closed as to be invisible to us or whether a fresh opening is made at each discharge. The processes of digestion, absorption, dissimilation, excretion, respiration, and growth are so similar to those described for *Amœba* that they need not be considered further at this place

**Reproduction.** — *Paramœcium* reproduces only by simple *binary division*. This process is interrupted occasionally by a temporary union (*conjugation*) of two individuals and a subsequent mutual fertilization.

*Binary fission.*

— In binary fission the animal divides transversely (Fig. 55). The first indication of a forthcoming division is seen in the micronucleus, which undergoes a sort of mitosis, its substance being equally divided between the two daughter nuclei; these separate and finally come to

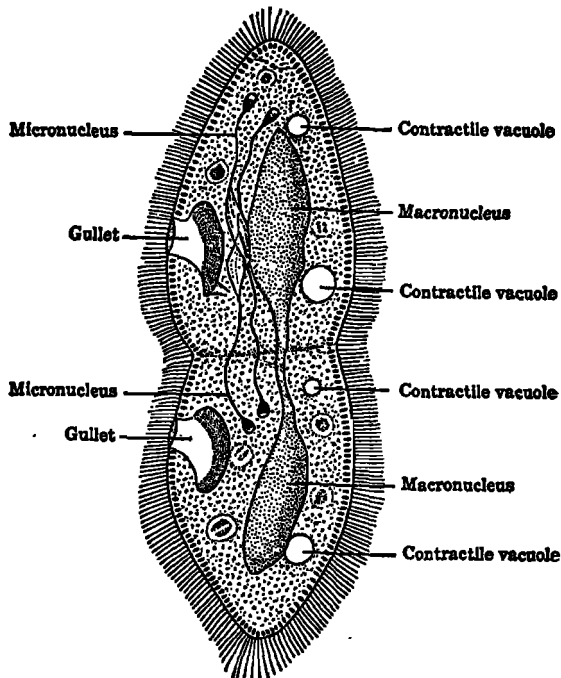


FIG. 55. — *Paramœcium aurelia*: binary fission.  
(From Newman after Lang.)

lie one near either end of the body. Figure 55 shows two dividing micronuclei, since there are two of these in *Paramœcium aurelia*. The macronucleus elongates and then divides transversely. The cytopharynx produces a bud which develops into another cytopharynx; these two structures move apart, the old cytopharynx advancing to the ventral middle line of the forepart of the body, and the new one to a similar position in the posterior half. The undulating membrane remains with the old cytopharynx while a new one arises in connection with the

new cytopharynx. A new contractile vacuole arises near the anterior end of the body, another just back of the middle line. While these events are taking place a constriction appears near the middle of the longitudinal diameter of the body; this cleavage furrow becomes deeper and deeper until only a slender thread of protoplasm holds the two halves of the body together. This connection is finally severed and the two daughter *Paramæcia* are freed from each other. Each contains both macro- and micro-nuclei, two contractile vacuoles, and a cytostome with cytopharynx. The entire process occupies about two hours. The time, however, varies considerably, depending upon the temperature of the water, the quality and quantity of food, and probably other factors. The daughter *Paramæcia* increase rapidly in size, and at the end of twenty-four hours divide again if the temperature remains at from 15°–17° C.; if the temperature is raised to 17°–20° C., two divisions may take place in one day.

Encystment of *Paramæcium* has been described, but if it really occurs, it apparently is a rare phenomenon.

*Conjugation.* — At a certain time in the life cycle of *Paramæcium* conjugation occurs. The conditions that initiate this process are not yet known, but the complicated stages have been quite fully worked out. When two *Paramæcia*, which are ready to conjugate, come together, they remain attached to each other because of the adhesive state of the external protoplasm. The ventral surfaces of the two animals are opposed, and a protoplasmic bridge is constructed between them. As soon as this union is effected, the nuclei pass through a series of stages which have been likened to the maturation processes of metazoan eggs. Reference to figure 56 will help to make clear the following description. Two micronuclei are present in this species. The micronuclei (*A*) grow larger, their chromatin breaking up into granules which radiate from a division center at one end. The nucleus then lengthens, forming a spindle, and subsequently divides into two (*B*). These immediately divide again without the intervention of a resting stage. The resultant eight nuclei (*C*) have been compared to the sperms produced by primary spermatocytes or to eggs with their polar bodies, and the divisions are considered as the first and second maturation mitoses. Reduction occurs, at least in part, at the second maturation division. Seven of the eight nuclei degener-

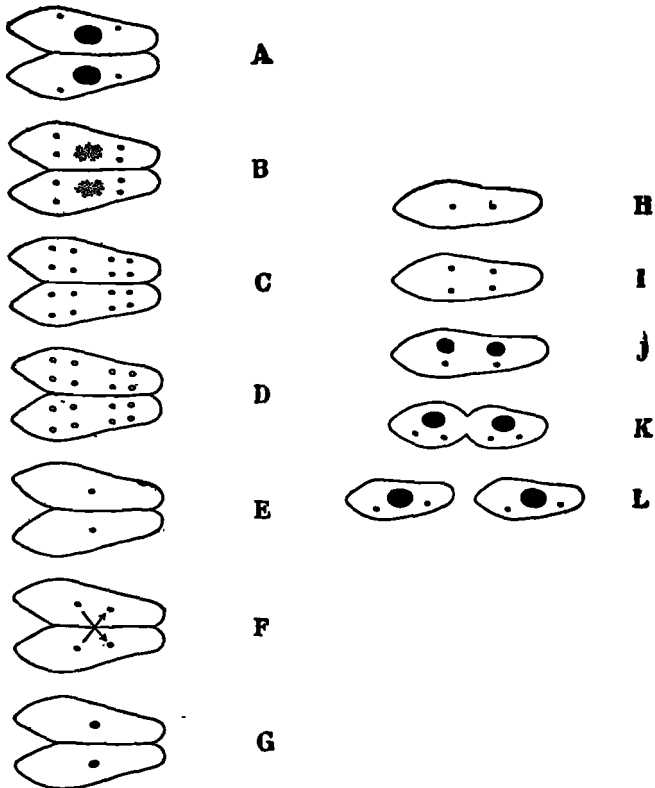


FIG. 56. — *Paramacium aurelia*: conjugation. A, union of two individuals along the peristomal region. B, degeneration of macronucleus and first division of the micronuclei. C, second division of micronuclei. D, seven of the eight micronuclei in each conjugant degenerate (indicated by circles) and disappear. E, each conjugant with a single remaining micronucleus. F, this nucleus divides into a stationary micronucleus and a migratory micronucleus — the gametic nuclei. The migratory micronuclei are exchanged by the conjugants and fuse with the respective stationary micronuclei to form the synkarya. This is fertilization. G, conjugants, with synkarya, separate (only one is followed from this point). H, first division of synkaryon to form two micronuclei. I, second reconstruction division. J, transformation of two micronuclei into macronuclei. K, division of micronuclei accompanied by cell division. L, typical nuclear condition restored. (After Woodruff.)

ate (*D*), the eighth divides again. During this division there are no definite spindle fibers and no longitudinal splitting of the chromosomes, but the granules of chromatin contained in the nuclei separate into two groups, one smaller than the other (Figs. 56, *E*; 57, *A*). These groups of chromatic material then become recognizable as distinct nuclei. The smaller nucleus might be

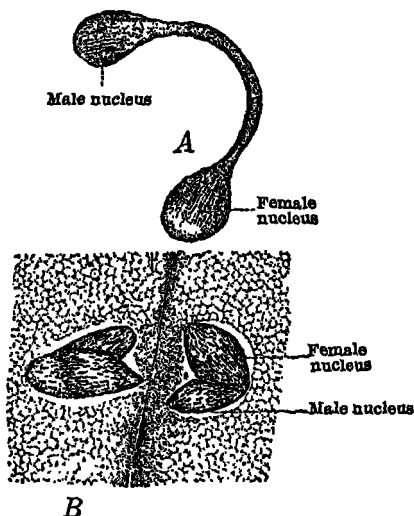


FIG. 57. — *Paramecium*: two views of the micronuclei during conjugation. A, the spindle formed during the division of the micronucleus which results in the production of a large female nucleus and a smaller male nucleus. B, the fusion of the male nucleus of one conjugant with the female nucleus of the other conjugant. (From Calkins and Cull.)

be considered comparable to the male nucleus, the other the female. The male nucleus migrates across the protoplasmic bridge between the two animals (Fig. 56, *F*) and unites with the female nucleus of the other conjugant (Figs. 56, *G*; 57, *B*), forming a fusion nucleus (Fig. 56, *G*). Thus is fertilization effected.

The conjugants separate soon after fertilization. The fusion nucleus of each conjugant, shortly after separation, divides by mitosis into two (*H*), and these two into four (*I*). Two of these increase in size and develop into macronuclei (*J*). The whole animal then divides by binary fission (*K*), each daughter cell securing one macronucleus and two mi-

cronuclei (*L*). An indefinite number of generations are produced by the transverse division of the two daughter cells resulting from each conjugant.

In a culture under continual observation a decline in the rate of reproduction occurs. The protoplasm at this stage undergoes a change both physically and chemically; the surface layer becomes sticky, so that when two cells meet they fuse, and conjugation results. This frequently occurs in a large number of animals in a single culture at the same time and a so-called "epidemic" of conjugation may then be observed. The conjugants are smaller

than the other specimens, being only .21 mm. long, while the usual length is about .3 mm.

If the *Paramæcia* are kept in a constant medium, e.g. hay infusion, they undergo a period of physiological depression about every three months, as shown by the decrease in their rate of division. Semi-annual periods also occur, but recovery from these does not take place if the animals are kept under constant conditions or conjugation is prevented, but the protoplasm degenerates and becomes vacuolated and the animals lose their energies and finally die.

Experiments have been performed which seem to show that in a varied environment neither conjugation nor death from old age necessarily occur. Thus Woodruff has carried a culture of *Paramæcia* through a period of over twenty years by changing the character of the medium daily without the intervention of conjugation. During this time there were over twelve thousand generations. The cycle may thus be prolonged by employing a varied culture medium. Since in nature the stimuli derived from changes in the environment probably are present, the length of the cycle may perhaps be prolonged indefinitely.

Conjugation within a clone of *P. aurelia* may result in diverse biotypes. These biotypes may differ in vigor, rate of multiplication, size, form and in other slight but constant diversities. Many phenomena that have been noted in *Paramæcium* may be due to gene mutations which appear to take place in both macronucleus and micronucleus. These include increased variation after endomixis, the effectiveness of selection within a clone, gain or loss of resistance to adverse environmental conditions, mortality, the production of abnormalities during vegetative reproduction, etc.

*Endomixis*. — A very interesting phenomenon that occurs in *Paramæcium* is termed endomixis. In *Paramæcium aurelia* definite rhythms in division rate have been noted and the organisms regularly every 40 or 50 generations replace their old macronucleus with a new one derived from the micronucleus. In other words, the active vegetative macronucleus is regularly replaced by chromatin from the reserve micronucleus, just as in conjugation, except that there is no admixture of any foreign chromatin. During this process the macronucleus breaks down (Fig. 58, B) and the micronuclei undergo two divisions (B, C). Six of these disintegrate (D) and the *Paramæcium* then divides, each daughter

receiving one micronucleus (*E*). This micronucleus then divides twice (*F*, *G*) and two of the resultant four micronuclei develop into macronuclei (*H*). The micronuclei divide again and the entire *Paramæcium* then divides, resulting in two daughters each

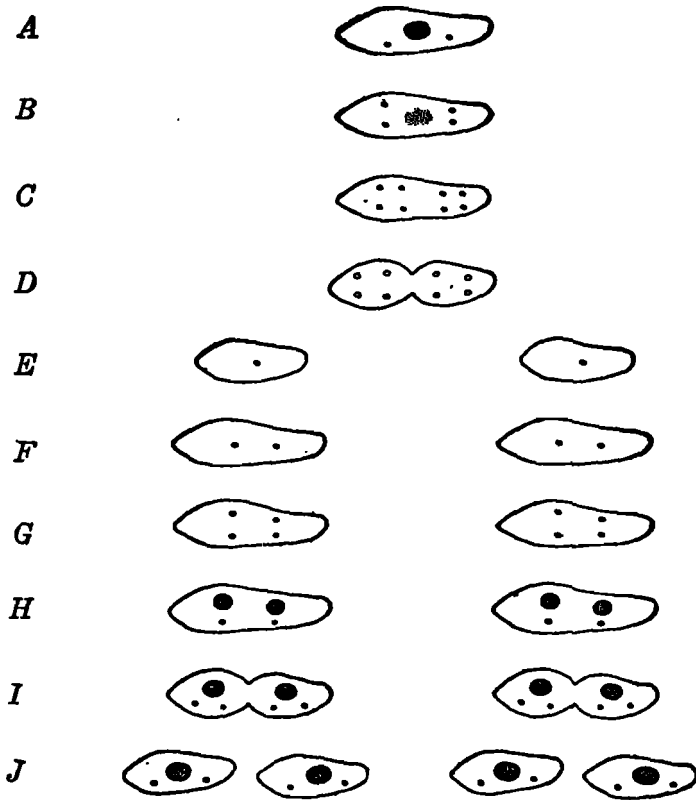


FIG. 58. — *Paramæcium aurelia*: diagram of the nuclear changes during endomixis. A, typical nuclear condition. B, degeneration of macronucleus and first division of micronuclei. C, second division of micronuclei. D, degeneration of six of the eight micronuclei. E, division of the cell. F, first reconstruction micronuclear division. G, second reconstruction micronuclear division. H, transformation of two micronuclei into macronuclei. I, micronuclear and cell division. J, typical nuclear condition restored. (From Woodruff.)

with one macronucleus and two micronuclei. Endomixis occurs also in *Paramæcium caudatum* and in certain other ciliates. Endomixis apparently brings about a physiological stimulation in the organism similar to that following conjugation.

**Behavior.** — *Paramæcium* is a more active animal than *Amæba*, swimming across the field of the microscope so rapidly that careful observations are necessary to discover the details of its movements. As in *Amæba*, its activities are either *spontaneous*, that is, initiated because of some internal influence, or result from some *external stimulus*. This stimulus is in all cases a *change in the environment*. For example, if a drop of distilled water is added to a drop of ordinary culture water containing a number of *Paramæcia*, all of the animals will enter and remain in the distilled water; they are stimulated to a certain kind of activity by the change in the composition of the water. They will soon become acclimated to their new surroundings, and will behave themselves within the distilled water in a normal manner until another change in their environment stimulates them to further reactions.

**Avoiding reaction.** — *Paramæcium* responds to stimuli either *negatively* or *positively*. The negative response is known as the

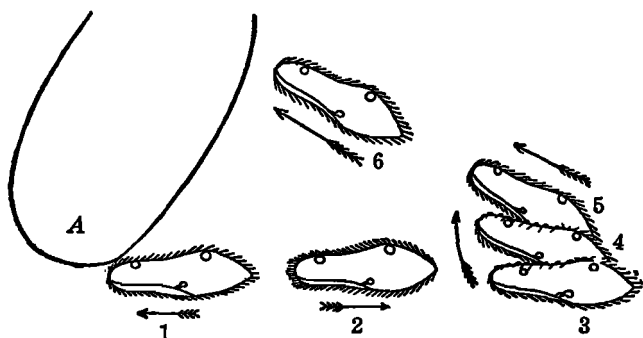


FIG. 59. — *Paramæcium*: diagram of the avoiding reaction. A is a solid object or other source of stimulation. 1-6, successive positions occupied by the animal. (The rotation on the long axis is not shown.) (From Jennings.)

“avoiding reaction”; it takes place in the following manner. When a *Paramæcium* receives an injurious stimulus at its anterior end, it reverses its cilia and swims backward for a short distance out of the region of stimulation; then its rotation decreases in rapidity and it swerves toward the aboral side more strongly than under normal conditions. Its posterior end then becomes a sort of pivot upon which the animal swings about in a circle (Fig. 59). During this revolution samples of the surrounding medium are brought into the oral groove. When a sample no longer contains the stimulus, the cilia resume their normal beating and the animal moves



forward again. If this once more brings it into the region of the stimulus, the avoiding reaction is repeated; this goes on as long as the animal receives the stimulus. The repetition of the avoiding reaction is very well shown when *Paramæcium* enters a drop of  $\frac{1}{10}$  per cent acetic acid. In attempting to get out of the drop the surrounding water is encountered; to this the avoiding reaction is given and a new direction is taken within the acid, which of course leads to the water and another negative reaction. Figure 60, B shows part of the pathway made by a single *Paramæcium* under these conditions.

*Positive reaction to chemicals.* — If a little acid is placed in the center of a large drop of water containing a number of *Paramæcia*, all of the animals in the drop will sooner or later encounter the acid, and having once entered are unable to escape, just as in

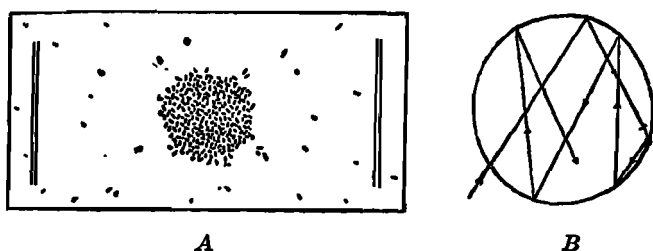


FIG. 60. — *Paramæcium*: positive reaction to acids. A, collection of *Paramæcia* in a drop of  $\frac{1}{10}$  per cent acetic acid. B, path followed by a single *Paramæcium* in a drop of acid showing mechanism of the collection shown in A. Each time the organism comes to the boundary of the acid it gives an avoiding reaction. (From Jennings.)

the case described above. A group is therefore formed in the acid, illustrating what is called a positive reaction (Fig. 60, A). This experiment may be repeated using a  $\frac{1}{2}$  per cent solution of common salt in which are placed a number of specimens. If a drop of  $\frac{1}{10}$  per cent solution of the same chemical is now added, the *Paramæcia* will swim into and directly across it, but on reaching the boundary between the two solutions on the other side of the drop, the avoiding reaction will be given. Soon the weaker solution will contain all of the animals which, having once entered, cannot escape. In many cases, as above, the passage from a strong solution to a weak solution causes no reaction. For certain substances, however, there is a definite strength which seems to suit the *Paramæcium* better than any other, and no reaction takes place on

entering it. Passage from such a solution to either a weaker or a stronger calls forth the avoiding reaction. The concentration is therefore called the "optimum."

"For each chemical there is a certain optimum concentration in which the *Paramæcia* are not caused to react. Passage from this optimum to regions of either greater or less concentration causes the avoiding reaction (Fig. 61), so that the animals tend to remain in the region of the optimum, and if this region is small, to form here a dense collection."

**Contact.** — *Paramæcia* may give any one of three reactions to contact stimuli; the first two are negative, the third positive. (1) If *Paramæcium* swims against an obstacle, or if the anterior end, which is more sensitive than the other parts of the body, is touched with a glass rod, the avoiding

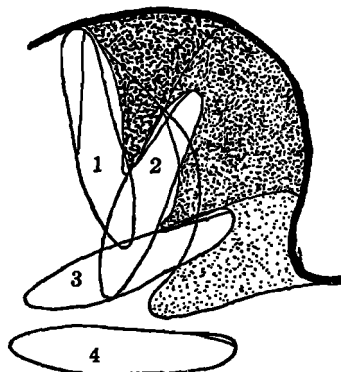


FIG. 61. — *Paramæcium*. Weak avoiding reaction as a result of contact with acidified ink. 1, 2, 3, 4, successive positions and final escape. (After Mast and Lashley.)

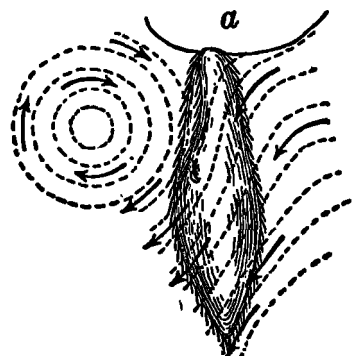


FIG. 62. — *Paramæcium* at rest with anterior end against a mass of bacteria (a), showing the currents produced by the cilia. (From Jennings.)

reaction is given. (2) When any other part of the body is stimulated in a like manner, the animal may simply swim forward. (3) Frequently a *Paramæcium*, upon striking an object when swimming slowly, comes to rest with its cilia in contact with the object (Fig. 62). This positive reaction often brings the animals into an environment rich in food.

**Light.** — *Paramæcia* do not respond in any way to ordinary visible light, but give the avoiding reaction when ultra-violet rays are thrown upon them; if unable to escape, death ensues in from ten to fifty seconds.

**Temperature.** — The optimum temperature for *Paramæcium* lies, under ordinary conditions, between 24° and 28° C. A num-

ber of animals placed on a slide, which is heated at one end, will swim about in all directions, giving the avoiding reaction where stimulated, until they become oriented so as to move toward the cooler end. This is the method of *trial and error*, that is, the animal tries all directions until the one is discovered which allows it to escape from the region of injurious stimulation.

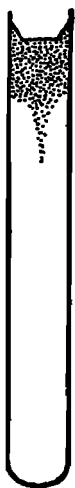


FIG. 63. — *Paramæcia* collected at the top of a vertical tube. (From Jennings after Jensen.)

*Gravity.*— Gravity in some unknown way causes *Paramæcia* to orient themselves with their anterior ends pointed upward. This brings them near the surface of the water. If a number are equally distributed in a test tube of water, they will gradually find their way to the top (Fig. 63). The most probable theory to account for this is that the substances within the body, being of different specific gravities, move about when the animal changes its position and act as stimuli, relief being obtained only when the animal has placed its body with its long diameter perpendicular to the earth's surface and its anterior end up. Under certain conditions *Paramæcium* are positive to gravity.

*Currents.*— If *Paramæcia* are placed in running water, they orient themselves with the anterior ends upstream and swim against the current. This is probably caused by the interference of the current with the beating of the cilia, for as soon as an animal reaches a position with anterior end upstream, the water no longer tends to reverse the cilia.

*Electric current.*— *Paramæcia* may be subjected to an electric current in the laboratory. A weak current causes a movement toward the cathode; a strong current reverses the direction of the beating of the cilia and causes the animals to swim backward toward the anode. Many other interesting phenomena might be cited, but the entire subject is too complex for brief discussion.

Frequently *Paramæcium* may be stimulated in more than one way at the same time. For example, a specimen which is in contact with a solid, is acted upon by gravity and may be acted upon by chemicals, heat, currents of water, and other stimuli. It has been found that gravity always gives way to other stimuli, and that if

more than one other factor is at work the one first in the field exerts the greater influence.

Both the spontaneous activities and reactions due to external stimuli are due to changes in the internal condition of the animal. The *physiological condition* of *Paramæcium*, therefore, determines the character of its response. This physiological state is a dynamic condition, changing continually with the processes of metabolism going on within the living substance of the animal. Thus one physiological state resolves itself into another; this becomes easier and more rapid after it has taken place a number of times, giving us grounds for the belief that stimuli and reactions have a distinct effect upon succeeding responses.

"We may sum up the external factors that produce or determine reactions as follows: (1) The organism may react to a *change*, even though neither beneficial nor injurious. (2) Anything that tends to interfere with the normal current of life activities produces reactions of a certain sort ('negative'). (3) Any change that tends to restore or favor the normal life processes *may* produce reactions of a different sort ('positive'). (4) Changes that in themselves neither interfere with nor assist the normal stream of life processes may produce negative or positive reactions, according as they are usually followed by changes that are injurious or beneficial. (5) Whether a given change shall produce reaction or not often depends on the completeness or incompleteness of the performance of the metabolic processes of the organism under the existing conditions. This makes the behavior fundamentally regulatory."

**Heredity in *Paramæcium*.** — Most of the complex phenomena of life are exhibited by the one-celled animals, and it is not strange to find that the offspring of the Protozoa resemble their parents. This "resemblance of child to parent" is called *heredity*. The descendants of a living organism are not exact copies of the progenitor, but differ in various minor details; "the difference between child and parent is called *variation*." *Paramæcium* has been made the subject of a thorough test with regard to hereditary phenomena by Professor Jennings. This investigator studied and measured over ten thousand *Paramæcia* which were carefully bred in the laboratory. In a "wild" lot of *Paramæcia* eight distinct races were found. Each race consisted of individuals, which, though affected by their environment, maintained a certain average size which was inherited. Characteristics that were acquired by the *Paramæcia*

were not handed down to their offspring, but were lost when the animals were reorganized during reproduction. It is thus the "fundamental constitution of the race," and not the various external influences, which determine the characteristics of each new generation.

## (2) OTHER INFUSORIA

The INFUSORIA are characterized by the possession of cilia during a part or whole of their life cycle. In most of them, also, the nuclear material is separated into a large macronucleus and a smaller micronucleus. Most of the INFUSORIA are free-living in fresh water or the sea. Many of them, however, are ectoparasites or endoparasites of man and other vertebrates and invertebrates. The INFUSORIA may conveniently be separated into two subclasses, the CILIATA and the ACINETARIA or SUCTORIA. The CILIATA possess cilia in both young and adult stages and the SUCTORIA, in the young stages only, the adults being provided with tentacles. By some authorities the ciliates are separated into the PROTOCILIATA containing the family OPALINIDÆ, and the EUCILIATA including the rest of the subclass. The four orders of ciliates are separated from one another on the basis of the character and distribution of their cilia.

**Order HOLOTRICHIDA.** — The species in this order possess cilia of approximately equal length all over the body, forming a continuous, evenly distributed coat in more primitive forms; but arranged in bands or restricted to special regions in more specialized forms. In some species the cytostome is a simple pore leading into a straight cytopharynx without cilia or undulating membranes, but often with a rod-apparatus by which the cytostome is closed and opened for food ingestion. In other species the cytostome is at the bottom of a peristomial depression leading into a short cytopharynx never supported by a rod-apparatus, but containing an undulating membrane; consequently the cytostome is not capable of being closed, but remains permanently open.

**Family OPALINIDÆ.** — This is an interesting group of INFUSORIA that are very common in the rectum of frogs, toads, and tadpoles. There are four genera, namely *Protoopalina* (Fig. 64, *a*), with a cylindrical binucleate form, *Zelleriella* (Fig. 64, *c*), with a flattened binucleate form, *Cepedea* (Fig. 64, *b*), with a cylindrical multinucleate form, and *Opalina* (Fig. 64, *d*), with a flattened multinucleate

form. These are all characterized by a covering of cilia of equal length arranged in parallel rows, by the absence of a cytostome and by the presence of only one type of nucleus. The nuclei, however, are of considerable interest since in some species, during mitosis, two types of chromosomes have been observed, large chromosomes that lie near the surface of the mitotic spindle and smaller chromosomes, in the form of slender rows of granules, in the center of the

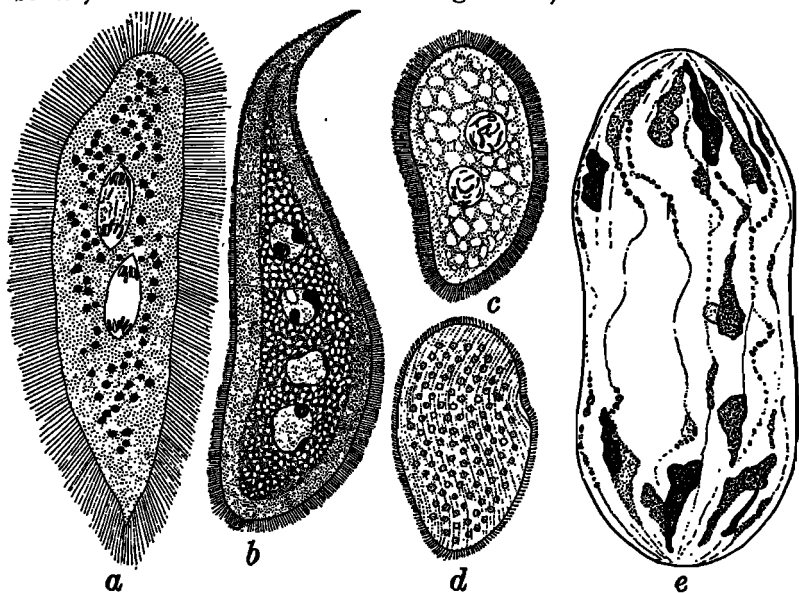


FIG. 64. — OPALINIDÆ. a, *Protoopalina*, a binucleate species; nuclei in anaphase of mitosis. b, *Cepedea lanceolata*, a quadrinucleate species. c, *Zelleriella macronucleata*, a binucleate species; nuclei in prophase of mitosis. d, *Opalina ranarum*, a multinucleate species. e, Nucleus of *Opalina* in anaphase of mitosis showing large, flat, "trophic" chromosomes, and small, linear, "reproductive" chromosomes. (After Metcalf.)

mitotic figure (Fig. 64, e). These two types of chromosomes may represent the material of the macronucleus and micronucleus, respectively, of other INFUSORIA. Another interesting characteristic of the OPALINIDÆ is the fact that in many species the nuclei come to rest in some stage of mitosis. The number of nuclei in the individuals of various species ranges from two to several thousand.

*Opalina ranarum* (Fig. 64, d), which lives in the rectum of the frog, is the commonest and best-known species. When alive it is opalescent in appearance. Some specimens reach a length of about

a millimeter and may be seen with the naked eye. The body contains a large number of spherical nuclei evenly distributed throughout the cytoplasm. Many small spindle-shaped bodies of unknown character are present in the endoplasm. Reproduction is by binary

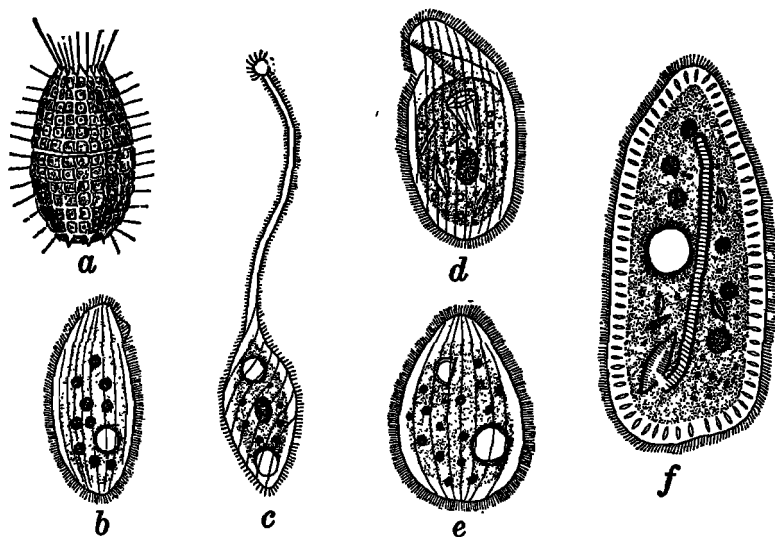


FIG. 65. — Free-living HOLOTRICHIDA. a, *Coleps hirtus*. b, *Colpidium cucullus*. c, *Lacrymaria olor*. d, *Chilodon cucullulus*. e, *Glaucoma scintillans*. f, *Frontonia leucas*. (a, after Conn; b-f, after Wang.)

division during most of the year, but in the spring rapid division results in the production of many small individuals which encyst and pass out in the fæces of the frog. These cysts when ingested by

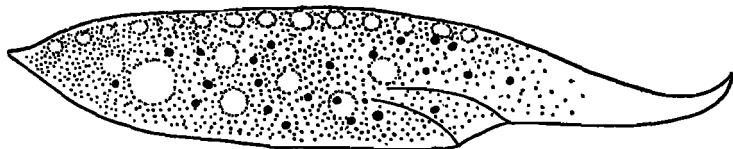


FIG. 66. — *Dileptus gigas*, a holotrich with many micronuclei (the larger black spherical bodies) and a macronucleus distributed in small granules throughout the endoplasm. (After Visscher.)

tadpoles, hatch in the rectum and give rise either to macrogametocytes or microgametocytes. The gametocytes, which contain from three to six nuclei, divide into uninucleate macrogametes or microgametes. These conjugate forming zygotes from each of

which a young opalina develops. *Opalina ranarum* may be kept alive outside of the body of the frog for as long as three days in Locke's solution.

**Free-living holotrichs.** — Bodies of fresh water, especially if decaying vegetation is present, contain great numbers of species and individuals belonging to this type. Some of the more interest-

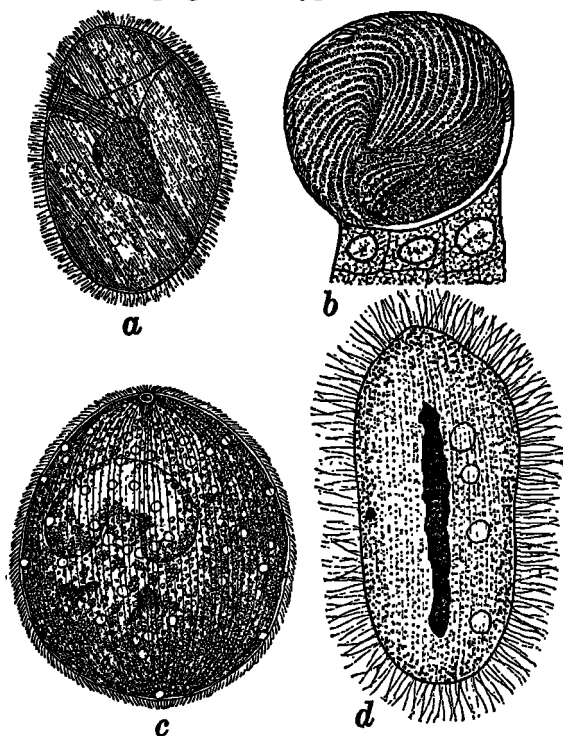


FIG. 67. — Parasitic HOLOTRICHIDA. a, *Isotricha intestinalis*, from the stomach of cattle. b, *Amphileptus branchiarum*, rounded up in gill of a frog tadpole. c, *Ichthyophthirius multifiliis*, from the skin of fish. d, *Anoplophrya marylandensis*, from the intestine of the earthworm. (a, after Becker; b, after Wenrich; c, after Bütschli; d, after Conkling.)

ing species are as follows. *Coleps hirtus* (Fig. 65, a) is a barrel-shaped species covered with twenty longitudinal rows of platelets and with three posterior spines. *Lacrymaria olor* (Fig. 65, c) is slender, 400 microns in length, and possesses a long, highly contractile proboscis. *Didinium nasutum* (Fig. 48) is barrel-shaped, has cilia restricted to two girdles, and a very expansible cytostome



at the end of a proboscis-like elevation. It feeds on *Paramæcium* and other ciliates which it engulfs whole. *Dileptus gigas* (Fig. 66) has many micronuclei and the chromatin of the macronucleus distributed in granules throughout the endoplasm. *Chilodon cucullulus* (Fig. 65, d) possesses a pharyngeal basket around the cytostome consisting of rod-shaped trichites. *Frontonia leucas* (Fig. 65, f) is a very large species about 300 microns in length. *Colpidium* (Fig. 65, b) is common in infusions; the oral surface is

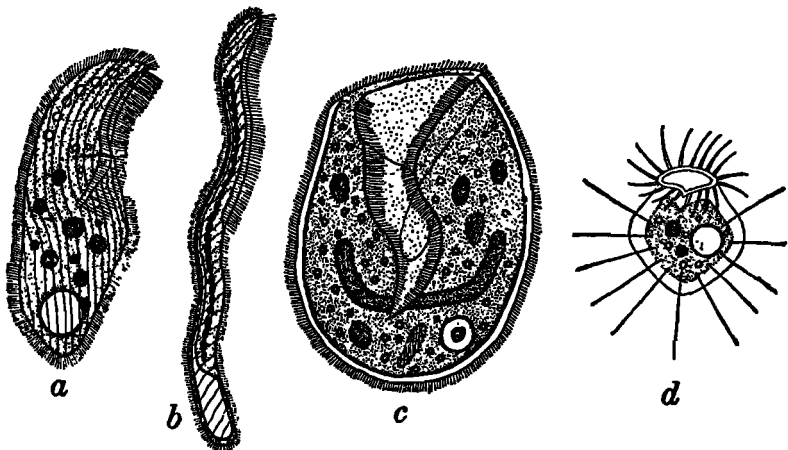


FIG. 68. — Free-living HETEROTRICHIDA. a, *Blepharisma lateritia*. b, *Spirostomum ambiguum*. c, *Bursaria truncatella*. d, *Halleria grandinella*. (After Wang.)

somewhat concave. A number of species of *Paramæcium* have been described; *P. aurelia* possesses two micronuclei; *P. multimicronucleatum* has four or more micronuclei; and *P. bursaria* contains ZOOCHLORELLÆ as symbionts. The eight species of *Paramæcium* may be separated into two groups according to the arrangement of their ventral cilia. There is a preoral and a postoral line or suture on the ventral surface against which the rows of cilia terminate. In the Caudatum group, consisting of *P. caudatum*, *P. aurelia*, and *P. multimicronucleatum*, the rows of cilia on the right side of the preoral suture run parallel to this line. In the Bursaria group, consisting of *P. woodruffi*, *P. trichium*, *P. bursaria* and *P. polycaryum*, none of the ventral rows are parallel to the preoral suture in the region anterior to the cytostome but bend toward and terminate against this line. (Lieberman.) Species belonging to

some of the genera mentioned above occur also in salt water and many species of holotrichs are exclusively marine.

**Parasitic holotrichs.** — Among the interesting parasitic species are the following. *Isotricha intestinalis* (Fig. 67, a) is an inhabitant of the stomach of cattle. *Buxtonella sulcata* lives in the cecum of cattle. *Entorhipidium echini* makes its home in the intestine of sea-urchins. *Lambornella stegomyia* parasitizes the larvæ of stegomyia mosquitoes. *Amphileptus branchiarum* (Fig. 67, b) spends part of its life in the gills of frog tadpoles. *Ichthyophthirius multifiliis* (Fig. 67, c) is a very large species that attacks the skin and gills of fresh-water fish often causing their death. *Anoplophrya marylandensis* (Fig. 67, d) lives in the intestine of the common earthworm.

**Order HETEROTRICHIDA.** — The HETEROTRICHIDA may have

cilia covering the entire body or they may be absent from certain regions but there is an adoral zone of either large cilia or membranelles. In the cytopharynx is a well-developed undulating membrane.

**Free-living heterotrichs.** — Many well-known ciliates living in fresh water and in the sea belong to this order. *Blepharisma lateritia* (Fig. 68, a) contains zoopurpurin which renders the body rose-red. *Spirostomum ambiguum* (Fig. 68, b) is a long slender species with a moniliform nucleus. *Bursaria truncatella* (Fig. 68, c) is a large broad species with a long curved, band-like macronucleus

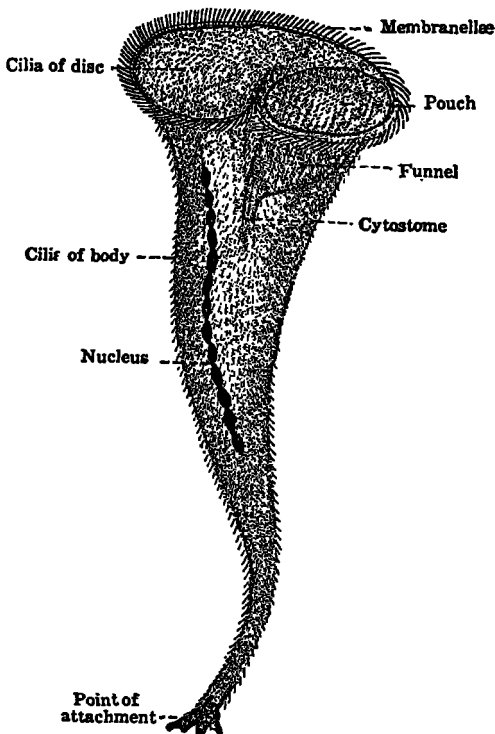


FIG. 69. — *Stentor coeruleus* in normal extended position as when attached to a solid object. (After Schaeffer.)

and many micronuclei. *Stentor polymorphus* lives either attached or free-swimming. When free-swimming it is oval or pyriform in shape; when attached it assumes a trumpet shape. Its body is usually green in color because of the presence of *Zoochorellæ*. *Stentor cœruleus* (Fig. 69) is bluish in color. *Halteria grandinella* (Fig. 68, d) is a small spherical species that is common in infusions. A girdle of long cilia near the center of the body enables it to perform springing movements.

**Parasitic heterotrichs.** — *Nyctotherus* and *Balantidium* are two interesting parasitic genera. Specimens of the genus *Nyctotherus*

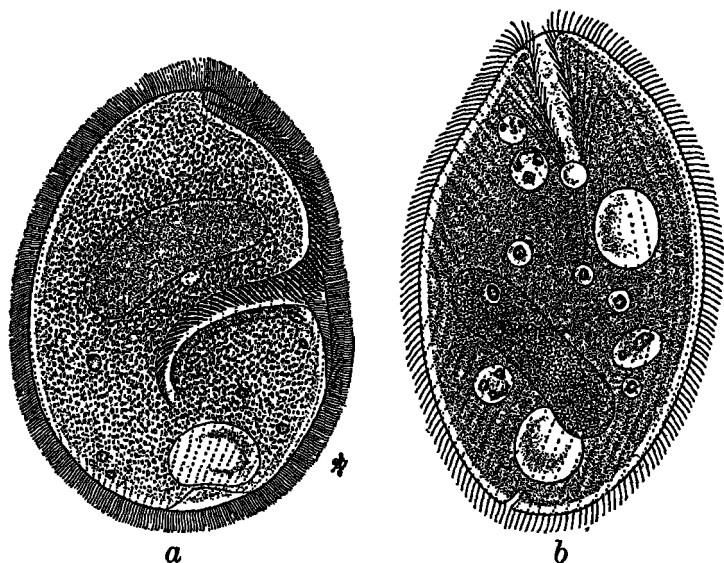


FIG. 70. — HETEROTRICHIDA: parasitic. a, *Nyctotherus cordiformis* from the rectum of the frog. b, *Balantidium coli* from the intestine of man. (After Wenyon.)

may easily be obtained for study from cockroaches and frogs. *N. ovalis* occurs in the intestine of cockroaches. The most common species in frogs is *N. cordiformis* (Fig. 70, a). This species has a long peristome extending from the anterior end to the center of the body and leading into a long curved cytopharynx. Other species occur in the frog, in myriapods, water beetles, crustaceans, crinoids, and fish.

*Balantidium* is also widely spread among animals having been recorded from frogs, salamanders, fish, coelenterates, flatworms,

sand fleas, cockroaches, snails, guinea-pigs, horses, ostriches, camels, etc. Of special importance is the species that lives in man, *B. coli* (Fig. 70, b), since it also lives in pigs and monkeys and is responsible for dysenteric conditions in its human host. *Balantidium coli* is present in about 80 per cent of the pigs in this country. It forms cysts which represent the infective stage

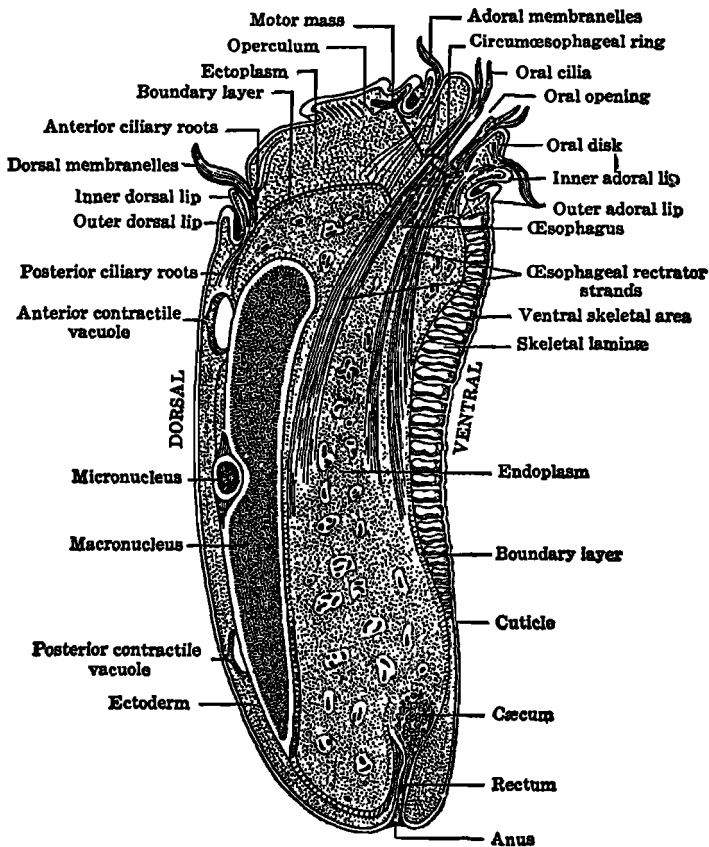


FIG. 71. — *Diplo-dinium ecaudatum*. Diagram to illustrate the neuromotor apparatus and complex structure of an infusorian. (After Sharp.)

and human beings probably become infected by swallowing cysts from pigs.

**Ciliates of cattle.**—The first and second stomachs of cattle, that is the rumen and reticulum, are highly infected with PROTOZOA, mostly ciliates. In this habitat two species of amœbæ, five

species of flagellates, and thirty-nine species and varieties of ciliates have been reported. These belong principally to the genera *Isotricha* (Fig. 67, a), *Bütschlia*, *Entodinium*, and *Diplodinium* (Fig. 71). From two to sixteen or more species of ciliates may be present in the stomach of one animal. They feed on bacteria, other PROTOZOA, and fragments of the host's food. They are obligatory parasites since they die quickly if removed from their habitat. Their exact relations to the host are not known; some or

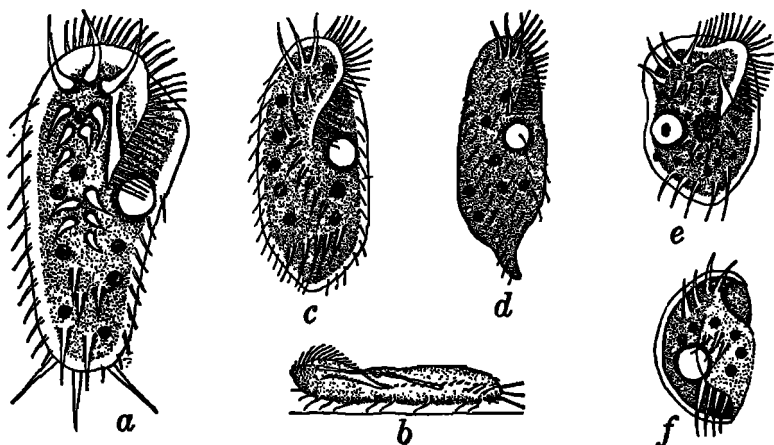


FIG. 72. — Free-living HYPOTRICHIDA. a, *Stylonichia mytilus*. b, *Stylonichia mytilus*. c, *Oxytricha bifaria*. d, *Uroleptus musculus*. e, *Euplotes charon*. f, *Aspidisca costata*. (a–f, after Wang; b, after Kent.)

all of them may be commensals or may assist in the digestion of the cellulose in the host's food and thus be symbiotic.

Among the ciliates of cattle are many species of great complexity. It is considered worth while to illustrate one of these here because protozoa are often erroneously considered to be simple organisms. The structure of *Diplodinium ecaudatum* is shown in figure 71 and sufficiently described in the legend of this figure. Of particular interest is the so-called neuromotor apparatus consisting of a central motorium which is connected with nerve rings and fibrils that make up a complicated system.

**Order HYPOTRICHIDA.** — The hypotrichs are typically modified for a creeping mode of life and are strikingly dorso-ventrally flattened with the ventral surface usually supplied with cirri — groups of cilia fused together — which are used as “legs” for creeping over the substratum. The peristomial groove is well

developed and possesses a very highly differentiated adoral zone of large cilia. The cytopharynx is supplied with an undulating membrane.

**Free-living hypotrichs** (Fig. 72). — Hypotrichs are common in infusions. Some of the species that may be encountered are as follows. *Oxytricha bifaria* (Fig. 72, c) occurs in both fresh and salt water; it has marginal cilia but no caudal cirri. *Uroleptus musculus*

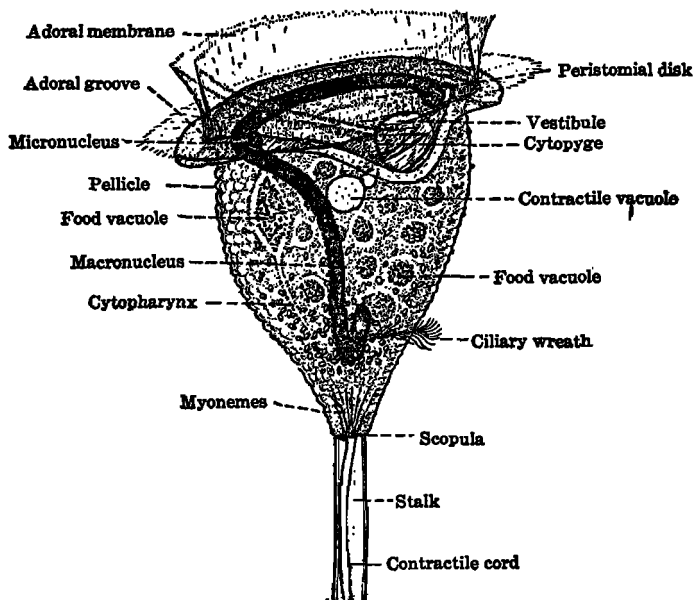


FIG. 73. — *Vorticella*. Diagram showing the structure of a typical specimen. (After Noland and Findley.)

(Fig. 72, d) has two median rows of cilia, three anterior cirri but no anal cirri. *Euplotes charon* (Fig. 72, e) has an ovoidal body ventrally flattened, nine or more large cirri opposite the oral groove and about nine cirri at the posterior end.

**Parasitic hypotrichs.** — *Kerona pediculus* is a good example of a hypotrichous ectoparasite. This species lives on the fresh-water polyp, *Hydra*, creeping about on the surface with untiring activity. It is dependent upon its host for food, but, besides the cells of the host, will ingest other PROTOZOA, especially euglenoids; the latter, however, are not ingested if the *Kerona* is detached from its host.

**Order PERITRICHIDA.** — With the exception of a few species, this order comprises forms highly specialized for a sedentary habit. Except in rare cases, the body cilia are completely absent. The feeding apparatus is highly specialized. The adoral spiral zone is wound around the peristomial disk which can be completely contracted over the mouth by means of myonemes on the margin. These *myonemes* are strands of cytoplasm specialized as contractile organelles. The adoral cilia are generally modified to form

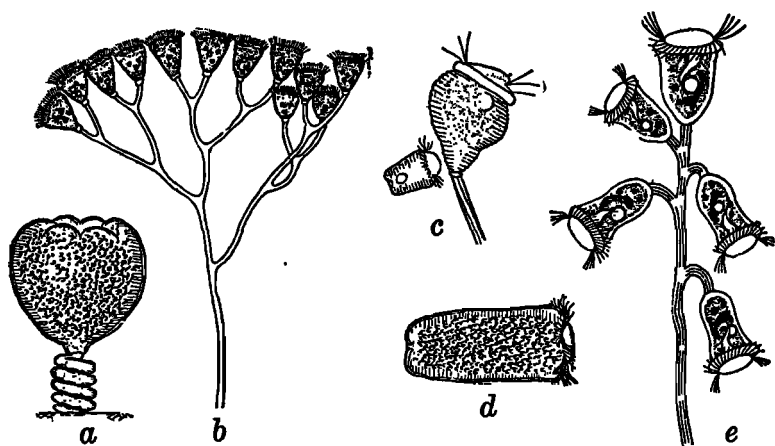


FIG. 74. — Free-living PERITRICHIDA. a, *Vorticella campanula*, contracted. b, *Epistylis flavicans*. c, *Vorticella striata* with sexual zooid. d, *Vorticella campanula*, telotroch or free-swimming swarm stage. e, *Carchesium polypinum*. (a, c, d, after Noland and Finley; b, e, after Wang.)

two undulating membranes which run parallel to each other. Instead of the adoral zone leading directly to the cytostome, it leads into a vestibule which is supplied with an undulating membrane and into which the anal pore and contractile vacuole as well as the cytostome open.

**Free-living peritrichs.** — Species of the genus *Vorticella* (Fig. 73) are common in fresh water. *Vorticella campanula* (Fig. 74, a, d) has a body shaped like an inverted bell, a contractile stalk, is always solitary, and yellowish or greenish in color. *Carchesium polypinum* (Fig. 74, e) is a colonial species with branching stalks that contract independently of one another. *Epistylis flavicans* (Fig. 74, b) is also colonial; its stalks are dichotomous and not contractile

**Parasitic peritrichs.** — A common species of parasitic peritrich is *Trichodina pediculus* (Fig. 75). It may be found gliding along on the surface of the body of the fresh-water *Hydra*, on tadpoles and other aquatic animals. Other species are ectozoic on the fresh-water flatworms of the genus *Planaria* and on the gills of certain fishes and mollusks. *Trichodina* is short and hour-glass-shaped, with a spiral band of adoral cilia leading into a cytopharynx, a ribbon-shaped nucleus, and one contractile vacuole. The

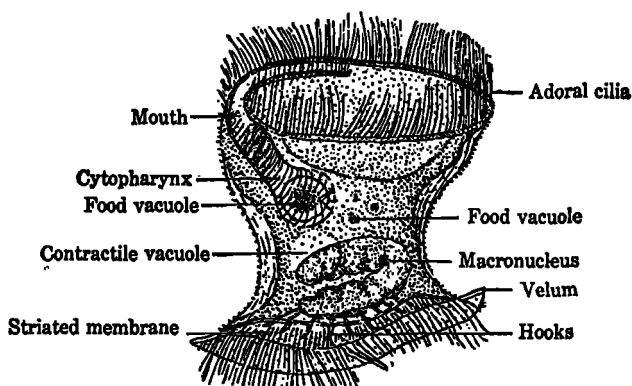


FIG. 75. — PERITRICHIDA. *Trichodina pediculus*, an ectozoic parasite that lives on *Hydra* and other aquatic animals. (After Clark.)

aboral surface is modified into a disk-like organ of attachment consisting of an inner ring of radially arranged teeth, an outer band of cilia, and a peripheral fold, the *velum*.

**Subclass SUCTORIA.** — The SUCTORIA or ACINETARIA are typically sedentary forms which are devoid of any ciliary mechanism in the "adult" stage and have no cytostome, but capture and ingest food by means of characteristic tentacles. They reveal their relationship to the CILIATA by the production of free-swimming ciliated larvæ, and by the possession of a typical infusorian nuclear apparatus consisting of separate macronuclei and micronuclei. All species possess capitate or suctorial tentacles each of which, as a rule, ends in a sucker-like knob. When a small animal, upon which the suctorian feeds, strikes the end of the tentacle, it is held fast by this sucker-like organ, and the general body substance of the prey is sucked down the tentacle into the body. Reproduction takes place typically by the formation of ciliated embryos which are formed from buds or processes constricted off from the



parent suctorían. After swimming around for a while the ciliated embryos settle down, become attached, and are transformed into typical suctoria.

**Free-living suctoria** (Fig. 76, 1-3).—Specimens belonging to this subclass are frequently encountered in vegetation gathered

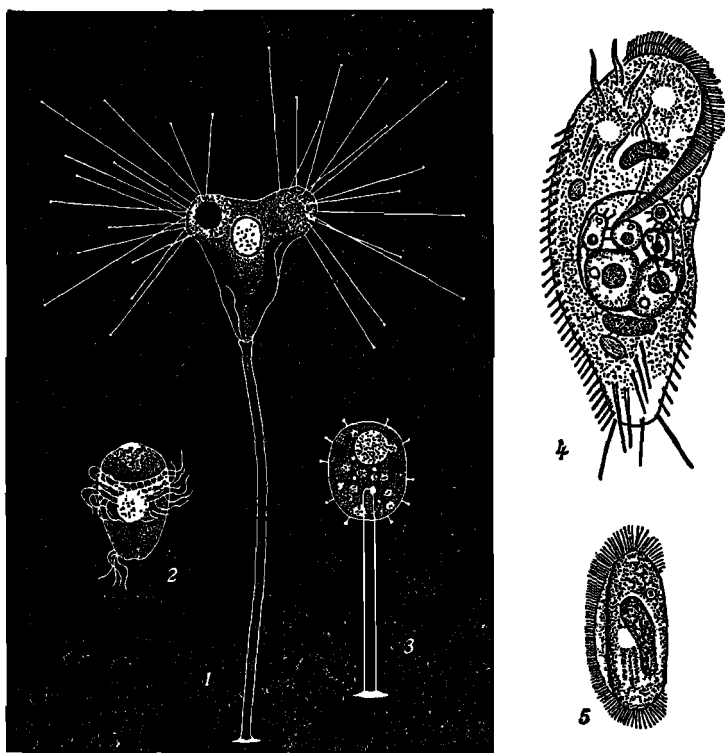


FIG. 76. — SUCTORIA. 1, *Tokophrya lemnae*: typical specimen. 2, *T. lemnae*: larva with four bands of cilia around body and a tuft of cilia at one end. 3, *T. lemnae*: larva after fixation, with pedicel and small tentacles. 4, *Sphaerophrya*: an endoparasitic species within a brood pouch in the body of a ciliate. 5, *Ophryodendron abietinum*: ciliated embryo. (1-3, after Noble; 4, after Stein; 5, after Martin.)

from ponds and in infusions. *Podophrya collini* is an American species with a stalk. *Sphaerophrya magna* has a spherical body without a stalk.

**Parasitic suctoria.** — Large numbers of ACINETARIA may be regarded as parasites in the broad sense of that term. Among these

are ectocommensals that attach themselves more or less regularly to some species of aquatic animal; for example, *Discophrya elongata* prefers the shells of gastropods. Endocommensals live in natural cavities in their hosts; for example, *Trichophrya salparum* lives in the pharyngeal cavities of certain tunicates. The true parasites also live both on the surface and in the interior of their hosts. *Ophryodendron abietinum* is an example of a true ectoparasite (Fig. 76, 5). The genus *Sphærophrya* includes endoparasites that live within the bodies of ciliates, such as *Stentor*, *Paramæcium*, and *Stylonychia* (Fig. 76, 4). A sort of brood pouch is formed within the host in which the "embryo" suctorian lives with tentacles retracted. Ciliated larvæ are formed in the brood pouch, separate from the host, and develop into free-living individuals.

## 5. PROTOZOA IN GENERAL

The knowledge of the morphology, physiology and classification of various types of PROTOZOA obtained from the study of the preceding pages makes it possible for us at this point to discuss some of the characteristics that are common to all PROTOZOA and to refer to some of the interesting biological facts and principles illustrated by this phylum.

**Habitats.** — PROTOZOA live in almost every conceivable type of habitat and their relations to their surroundings provide a fascinating study in ecology. As noted in the introduction (page 1), moisture is absolutely necessary for the continued existence of PROTOZOA, hence we find them in fresh-water streams and bodies of fresh and salt water of all sizes, in the soil to a depth of a foot or more, within the bodies of other animals and in fact in moist places almost everywhere. Those that live suspended in the water without access to the shore or bottom constitute a large part of the plankton. Many of them are temporarily or permanently attached to fixed or moving objects such as rocks or the bodies of aquatic animals. Shelled species are often unable to swim and must creep about on solid objects in the water. Each species is more or less restricted to a certain type of environment just as are higher animals. The PROTOZOA that are best known to students and teachers are those that appear when pond weed is brought into the laboratory and allowed to decay under fresh water. Less well known are the species included in fresh-water

and marine plankton, those that live in the soil and other moist places, and those that parasitize plants and other animals. The small size of PROTOZOA enables them to exist in minute spaces hence they are more ubiquitous than any other type of animal.

The number of species of PROTOZOA that one may expect to find is indicated by the observation that the surface water of a typical pond in the botanical gardens of the University of Pennsylvania during the period of one year contained 27 species of SARCODINA, 31 species of MASTIGOPHORA, and 109 species of INFUSORIA. (Wang.) The seasonal distribution of these organisms appeared to be influenced principally by temperature, the oxygen content and hydrogen-ion concentration of the water and the relative amount of dissolved acids in the water at different times of the year. The greatest number of most of the species occurred during September and October.

**General morphology.** — *Form and size.* — Every species of protozoon has a definite form and the size of the individuals vary within definite, usually narrow, limits. Even *Amœba proteus*, which is often erroneously described as a shapeless mass of protoplasm, has size and form characteristics that separate it from other species of amœbæ. Form is determined largely by the consistency of the cytoplasm, by the production of limiting membranes, shells, and skeletons, and by the character of the activities of the organisms. Thus the changes in shape of amœbæ are possible because of the absence of a cuticle, and the great elasticity of such species as *Euglena* and *Trichomonas* are the result of a thin cuticle. Shells and tests such as those of *Arcella* and *Diffugia* obviously determine the shape of those species that secrete them, and are so constant in form as to furnish excellent criteria for taxonomic purposes. The skeletons of some species are very elaborate structures of calcium carbonate or silica. Form is also correlated with the organism's mode of life. PROTOZOA that are suspended in the water are often spherical; those that move in a definite direction, such as *Paramœcium*, are ellipsoidal and the longer axis lies in the path of progression; attached species, like *Vorticella*, are more or less radial in symmetry; species that creep about on the surface of solid objects, such as *Oxytricha*, may be dorso-ventrally flattened; and a few species, as in *Giardia*, are bilaterally symmetrical. Size is a characteristic that is extraordinarily con-

stant. Anyone who has measured large numbers of individuals of a given species can appreciate this.

*Cytoplasm.* — The cytoplasm of PROTOZOA is mostly colorless but some species are tinted, for example *Stentor caeruleus*, which is blue, and *Blepharisma lateritia* which is rose-red. Two types of cytoplasm are usually distinguishable, the peripheral ectoplasm which is denser, hyaline, and homogeneous, and the central endoplasm which is more fluid and often granulated or alveolated. That these two types of cytoplasm may change from one to the other has been demonstrated in *Amæba proteus*, but in many species they appear to be persistent.

*Nuclei.* — Most PROTOZOA possess a single nucleus but many of them have two (*Arcella vulgaris*) or many (*Opalina ranarum*) of the same type, or two of different types (INFUSORIA in general). The characteristic shape of the nucleus is spherical but many other forms are common; for example, the oval nucleus of *Paramæcium*, the kidney-shaped nucleus of *Balantidium coli* and the moniliform nucleus of *Spirostomum*. There are two principal types of nuclei as regards structure, the vesicular type in which the chromatin is concentrated in a single mass or grain (*Arcella*); and the granular type in which the chromatin is distributed in grains throughout the entire nucleus (*Amæba*). While some protozoan nuclei may be described as strictly of the vesicular or granular type, the majority are intermediate in structure and partake of the characters of both types. The two types of nuclei possessed by INFUSORIA are known as macronuclei and micronuclei; the former contains trophochromatin and controls the vegetative functions and the latter contains idiochromatin and controls the reproductive processes of the organism. Among the other peculiar nuclear conditions exhibited by INFUSORIA are the distributed nucleus of *Dileptus*, in which the chromatin granules are scattered throughout the cytoplasm, and the combination nucleus of *Opalina* which contains a group of large chromosomes, trophic in function, and a second group of small chromosomes reproductive in function. As in higher animals the most important nuclear element is chromatin. In some PROTOZOA chromatin occurs in the form of granules, called chromidia, located in the cytoplasm either scattered or in a ring, as in *Arcella*. These chromidia are probably of nuclear origin.

*Nuclear division.* — The macronuclei of the INFUSORIA appear to divide usually by direct or amitotic division as in *Paramæcium*.

In a few species of PROTOZOA, for example in *Ephelota* among the ACINETARIA, the macronucleus branches and new nuclei arise by the pinching off of buds from these branches. But by far the majority of protozoan nuclei divide by some type of mitosis. Chromosomes arise, divide, and are equally distributed to the daughter cells as in metazoan cells. In some species mitosis occurs within the nuclear membrane.

*Vacuoles.* — Contractile vacuoles, food vacuoles, and stationary vacuoles containing fluid may be present in the bodies of PROTOZOA. The contractile vacuoles are generally considered ectoplasmic in origin. As a rule they are found in fresh-water species and are absent in a great many parasitic and marine forms. Their function appears to be to regulate the osmotic pressure of the cell by the elimination of a portion of the water which is constantly being taken into the cell by imbibition and osmosis. They are also concerned with the elimination of nitrogenous wastes and possibly with the elimination of carbon dioxide (respiration).

*Plastids and other inclusions.* — The principal inclusions that are of more or less constant occurrence in PROTOZOA are chromatophores, pyrenoids, stigmata, crystals, pigments, and symbiotic organisms. Chromatophores are characteristic of holophytic PROTOZOA. They vary in shape and number but are constant in these respects in the different species. They contain green chlorophyll but may be colored yellow, brown, or red by pigments. Pyrenoids are the centers around which are formed paramylum bodies. They may be free or embedded in chromatophores. Stigmata or eye spots are bodies colored red by pigment and often accompanied by a lens-like paramylum body. Pigments of various colors may be present in PROTOZOA. Thus malarial organisms elaborate a brownish pigment (melanin) as a product of the digestion of hæmoglobin. Crystals may also be constant inclusions in certain PROTOZOA. For example, several species of fresh-water amœbæ contain crystals that differ in shape from one another but are constant in shape for each species. Oil droplets are elaborated by some species, such as *Uroglæna*.

*Organelles of motion and locomotion.* — The ectoplasm is the layer which is in the most intimate contact with the environment and is the seat of the organelles of motion and locomotion. In the SARCODINA movement is effected by means of temporary extrusions of the protoplasm, called pseudopodia, which are always

formed from the ectoplasm although the endoplasm may flow in later. They are mainly of two types, viz., lobopodia and axopodia, of which the first are simply more or less fluid extrusions of the body, while the second possess a central supporting structure or axostyle. In the MASTIGOPHORA the organs of locomotion are vibratile thread-like processes called flagella. These flagella are comparatively long and usually few in number, and have probably arisen by a gradual transition from pseudopodia. Flagella may be divided into two types: tractella and pulsella. The first type is situated at the end which is anterior when the organism is in motion and drags the body along; the latter is generally situated posteriorly and pushes or propels the body forward. In a number of the parasitic flagellates, there is frequently a thin layer of protoplasm which connects a given flagellum, throughout the greater part of its length, with the body and is known as an undulating membrane. Cilia, which are the organs of locomotion in the class INFUSORIA, are also slender thread-like processes which differ from flagella chiefly in that they are very much smaller in comparison to the body of the protozoon, occur in much greater numbers, and differ in their type of movement. Cilia are generally arranged in rows, and there is a definite coordination between the beat of the individual cilia in each row. There are several modifications of the cilia, such as cirri, membranellæ, and undulating membranes. These are all produced by the fusion of a number of cilia. Mention should also be made of certain contractile elements known as myonemes, which are muscle-like and occur in the body of certain of the MASTIGOPHORA, INFUSORIA, and SPOROZOA.

*Organelles for the capture and ingestion of food.* — The organelles of locomotion also play the principal rôle in the capture and ingestion of food. Thus *Amœba proteus* engulfs solid food bodies and is even able to capture other PROTOZOA and cut in two such organisms as *Paramecium* and *Frontonia* by means of its pseudopodia. Holozoic flagellates that ingest solid particles, in many cases use their flagella to drive them into the cytostome. The ciliates possess the most complicated mechanism for capturing and ingesting food; this consists of cilia modified in length and arrangement or fused together into cirri or undulating membranes which may extend down into the cytopharynx. In the SUCTORIA tentacles are provided which paralyze organisms, usually ciliates, that come in contact with them and suck the protoplasm out of the prey and

pass it down into the endoplasm leaving very little but the periplast behind. Many other specialized structures are present among the PROTOZOA that aid in the capture and ingestion of food, such as the trichocysts of *Paramæcium* and the myonemes of *Vorticella*. Many free-living PROTOZOA and practically all of the parasitic PROTOZOA do not ingest solid particles and have no organelles for that purpose; they manufacture food by photosynthesis or absorb it through the surface of the body.

**General physiology. — Nutrition.** — The principal types of nutrition exhibited by PROTOZOA are holozoic, holophytic, and saprozoic. PROTOZOA, such as *Amæba* and *Paramæcium*, that feed on solid particles are said to be holozoic. As a rule, each species is capable of food selection, for example, the holotrichous ciliate, *Actinobolus radians*, pays no attention to many small ciliates and flagellates but immediately captures *Halteria grandinella* whenever an opportunity is afforded; and *Didinium nasutum* has a predilection for *Paramæcium*. The ingested food of holozoic PROTOZOA is confined in food vacuoles and digested and assimilated as described in *Amæba* and *Paramæcium*. Undigested material is cast out at any point on the surface, at a definite anal spot (*Paramæcium*), or through a permanent cytoproct (*Balantidium*).

Holophytic nutrition is particularly common among the PHYTOMASTIGINA. The exclusively holophytic forms (notably some of the PHYTOMONADIDA) require only the presence of sunlight, certain dissolved minerals, and CO<sub>2</sub> to build up and synthesize their complex food materials. Many of the other chromatophore-bearing species, however, live and reproduce much more readily in a medium containing some organic matter. Consequently they must, to a certain extent, be saprophytic. Certain species of PROTOZOA, such as *Paramæcium bursaria* and *Stentor polymorphus*, may obtain nutriment from the green algæ (*Zoochlorellæ*) that live within them.

Saprozoic nutrition involves the absorption through the general body wall or through some specialized region of the body of dissolved organic material in the medium. Dissolved proteins and carbohydrates resulting from the disintegration of plants and animals, as in an infusion, probably furnish the food for this type of organism. Many parasites, such as *Endamæba histolytica* and *Balantidium coli*, ingest solid particles and are thus holozoic, but they may also absorb through the body surface food digested by the host or the disintegrated protoplasm of the host. Other

parasites, such as *Opalina* and *Giardia*, do not possess any structural modifications for the ingestion of solid particles and must obtain all their nutriment by absorption.

*Secretion.* — Various types of secretions are produced by PROTOZOA. Some of them are as follows. The endoplasm of holozoic species secretes digestive ferments; SUCTORIA secrete a poison that paralyzes other INFUSORIA that come in contact with their tentacles; many species secrete shells (*Arcella*) or skeletons (*Radio-laria*); the pseudopodia of certain SARCODINA are mucilaginous (*Diffugia*) and enable the organisms to adhere to the substratum; arcellas secrete gas bubbles which lower their weight and bring them to the surface of the water; the parasite of amoebic dysentery (*Endamæba histolytica*) secretes a proteolytic enzyme which dissolves the cells of the intestinal wall of its human host; and SARCOSPORIDIA produce a toxic substance called sarcocystin.

*Excretion.* — Soluble waste materials are excreted either by diffusion through the general body surface, or, after accumulation in the contractile vacuole, by emptying from it to the exterior. Another very effective method of eliminating waste materials from the body is to throw them out of solution by precipitation. The crystals described in *Amæba proteus* and the pigment in *Actinosphærium* are probably of this nature. The melanin pigment of certain blood-inhabiting SPOROZOA is an insoluble waste formed from the digestion of hæmoglobin.

*Respiration.* — Respiration, in its broadest sense, includes any process by which an organism liberates the potential energy represented in the complex chemicals of its body. It may be effected either aerobically by oxidation or anaerobically by the splitting up of complex chemical substances into simple compounds. The end result, in either case, is the same. Practically all free-living PROTOZOA live in an environment containing more or less dissolved oxygen. Through the general body surface the animal absorbs the oxygen and eliminates the carbon dioxide and water which result from the oxidation. The contractile vacuole is probably also effective in eliminating these wastes. Many parasitic forms live in environments which are partially or totally lacking in oxygen. Here respiration must be of the anaerobic type.

*Circulation.* — The protozoan body is so small that the circulation of nutritive material, secretions, excretions, etc., takes place by streaming movements of the cytoplasm and hence no circulatory



system is necessary. Thus food vacuoles are distributed through the body of *Paramæcium* by cyclosis, and in a suctorian, the protoplasm of its prey passes through the tentacles and into the body.

*Motion and locomotion.* — Movements among the PROTOZOA are due to pseudopodia, flagella, cilia, and contractile elements such as myonemes. Amœboid movement has been described in *Amœba proteus*. As noted, pseudopodia are of two chief types — lobopodia and axopodia. The former are the common type and occur in the amœbæ. They consist of an extrusion of the body with no specific structural differentiation. Axopodia, on the other hand, found in such forms as *Actinophrys*, are capable of swinging or bending movements and possess a secreted axis which is either rigid or elastic in nature. MASTIGOPHORA move by means of flagella. The commonest type of flagellum is the tractellum, *i.e.* a flagellum which drags rather than propels the organism. In some species the entire length of the flagellum is thrown into motion and the organism may progress very rapidly, as in the hæmoflagellates; in other species only about one third of the distal end vibrates often causing the organism to progress in a series of jumps. In certain species, like *Peranema*, almost the entire flagellum is held stiff and only a very small part of the distal end moves. MASTIGOPHORA with flagella may move by means of pseudopodia, and some of the highly developed EUGLENOIDIDA, such as *Euglena*, periodically lose their flagella and move about by crawling along the substratum with a kind of rocking movement. Forms with a semi-resistant periplast, especially the EUGLENOIDIDA, often exhibit peristaltic waves of contraction which run down the length of the body. Such movements are termed metabolic, or euglenoid, since they are especially common in *Euglena*.

Movement among the INFUSORIA is effected by cilia. The action of cilia in locomotion has been described in *Paramæcium*. As a rule, cilia are situated in rows, and their movement is concerted. Each cilium contracts a short interval after the one in front of it and before the one behind it. Thus, viewed from the side, a moving row of cilia looks as if successive waves were passing over it. Furthermore, adjacent cilia of different rows beat in unison. When seen from above a ciliated surface has the appearance of a wheat field in the wind, *i.e.* successive waves fol-

low one another across the ciliated surface (Fig. 47). Hypotrichous ciliates are capable of swimming, but spend most of their time creeping on the substratum by means of cirri on the ventral surface which represent bunches of fused cilia and act practically as legs. In *Euplotes*, the cirri are aided in creeping by the peristomial membranelles.

**Behavior.** — The reactions of PROTOZOA to stimuli, which taken together constitute what is known as their behavior, have attracted much study. Some of the results have already been noted in *Amæba*, *Euglena*, and *Paramæcium*. In general the reaction of an animal to a stimulus involves three systems: first, a sense receptor; second, a conducting system; and third, an effector. Such structures are not visibly differentiated in forms like *Amæba*, but the portion of the body which receives the stimulus is also the one which reacts so that conduction is probably little more than a general diffusion of the stimulus through a localized portion of the body.

The flagellates have progressed markedly in the development of a reflex type of behavior (receptor-conductor-effector), due largely to the presence of definite organs of locomotion and more or less permanent body form. This is evident from a comparison of the behavior of *Amæba* and *Euglena*. Of special interest is the relation of the stigma to light stimulation.

The reflex type of reaction is developed to a much higher state in the INFUSORIA. The reactions of *Paramæcium* to various stimuli have already been described. In *Stentor* there is fairly clear evidence that one portion of the body receives the stimulus, that this is transmitted to definite cilia, which in turn produce a definite motor response. A number of investigators have endeavored to discover a definite fibrillar conduction-system in ciliates and flagellates. An account of this subject is presented on page 71.

In conclusion, we can do no better than to insert a quotation from Jennings. "All together, there is no evidence of the existence of differences of fundamental character between the behavior of the PROTOZOA and that of the lower METAZOA. The study of behavior lends no support to the view that the life activities are of an essentially different character in the PROTOZOA and the METAZOA. The behavior of the PROTOZOA appears to be no more and no less machine-like than that of the METAZOA; similar principles govern both."

**Reproduction.** — *Asexual reproduction.* — The common method of reproduction in the PROTOZOA is that of simple or binary fission. During this process first the nucleus, then the cytoplasm divides. In some cases the nucleus undergoes a series of divisions after which the body divides into as many parts as there are nuclei. Such a process is known as multiple fission. In other cases the division of the cytoplasm only takes place at special periods in the life cycle so that, as a result, the typical condition of the organism is that of a plasmodium. When division of such a plasmodium does take place, it generally forms two or more multinucleate bodies. Such a process is known as plasmotomy.

Budding is a type of asexual reproduction that occurs regularly in certain species. A bud is a part of the cytoplasm of the parent containing a nucleus of parental origin. Buds cut off from the outside of the parent are exogenous. This occurs, for example, in certain amoebæ (*Endamæba patuxent* of the oyster), in the ciliate *Noctiluca*, in SPOROZOA, and in *Ephelota* and other SUCTORIA. Endogenous or internal budding is not as common as the exogenous type. It consists in the separation of a mass of cytoplasm containing a nucleus from the rest of the organism within the body. It occurs commonly in certain SPOROZOA but rarely (or not at all) in the other classes of PROTOZOA.

*Sexual reproduction.* — Conjugation, or the temporary union of two individuals of the same species involving an exchange of nuclear material, accompanies sexual reproduction in many PROTOZOA, especially INFUSORIA. This process has been described fully in *Paramæcium*. When the conjugants are of the same size as in *Paramæcium*, they are said to be isogamous; when of different sizes, as in *Chilodon cucullulus*, anisogamous. The permanent union of two protozoan individuals is called copulation. The organisms that unite are usually smaller than normal vegetative individuals and are known as gametes. The gametes may be of the same size (isogamous) as in *Monocystis*, or may differ in size (anisogamous) as in *Plasmodium vivax*. In the latter case they correspond to the egg cells and spermatozoa of the METAZOA. The body formed by the fusion of two gametes is a zygote. The life cycles of many of the PROTOZOA, especially the SPOROZOA, are sometimes very complicated because of the types of sexual reproduction involved.

**Special morphology and physiology.** — Various topics of interest in connection with PROTOZOA are referred to briefly here. Further information may be found in books on Protozoology or in scientific journals.

*Colonial Protozoa and Metazoa.* — Although PROTOZOA are defined as unicellular animals many of them are colonial in habit and others at certain stages in their life cycles consist of many cells. The colonial forms, as we have seen, may consist of a variable number of cells irregularly arranged (*Carchesium*) or of a definite number arranged in a definite way (*Volvocidæ*). The members of the colony may be entirely independent, except for the common gelatinous matrix in which they are embedded (*Pandorina*), or may be connected by protoplasmic strands (*Volvox*). The cells may be of one kind (*Spondylomorom*) or may be differentiated into somatic cells and germ cells (*Volvox*). The somatic cells of PROTOZOA in general differ from somatic cells in the METAZOA since there is no histological differentiation among them and they are comparatively independent. Multicellular stages occur regularly in the life cycles of certain PROTOZOA. For example, in the gregarine, *Ophryocystis*, each member of a pair at the time of copulation divides into two cells, a small uninucleate gamete and a larger binucleate cell which forms a protecting envelope. It seems probable that the METAZOA evolved from the PROTOZOA through stages resembling somewhat the colonial PROTOZOA of to-day. Perhaps the most fundamental difference between protozoan and metazoan cells is the fact that the PROTOZOA are able with one cell to carry on all the life processes characteristic of the METAZOA; whereas metazoan cells are limited to special functions.

*Neuromotor apparatus.* — The term "neuromotor apparatus" has been applied to a system of connected fibrils centering in a differentiated mass of cytoplasm near the anterior end called the motorium. In a ciliate, *Diplodinium ecaudatum*, that lives in the rumen of cattle, a fibril connects the motorium with a circum-oesophageal ring which encircles the gullet. From this, other fibrils lead posteriorly along the gullet. There are also fibrils running to the bases of the adoral membranelles and to the operculum. Similar systems of fibrils have been described in *Paramecium* and in a number of other ciliates and in many flagellates. Special technical methods are necessary to reveal these fibrils. Micro-

dissection experiments indicate that the activities of the organism are coordinated by the neuromotor system. For example, when the motorium is destroyed uncoordinated movements of the membranelles result.

*Conjugation and endomixis.* — The significance of conjugation cannot be definitely stated. Some investigators believe that *Paramæcium* and other ciliates pass through a life cycle containing three distinct stages. The period of (1) youth is characterized by rapid cell multiplication and growth; (2) maturity, by less frequent cell division, sexual maturity, and the cessation of growth; and (3) old age, by degeneration and natural death. Death is avoided by conjugation, which rejuvenates the senescent animals.

Jennings has shown that some *Paramæcia* conjugate more often than others, and Woodruff has succeeded in carrying a culture through a period of over twenty years without conjugation. During this time there were over twelve thousand generations. These facts "weaken the theory that conjugation is to be considered the result of senile degeneration at the end of the life cycle," and show that this protozoon "has unlimited power of reproduction without conjugation or artificial stimulation" if given a favorable environment. It may be noted at this point that Weismann many years ago suggested that PROTOZOA do not die a natural death since the two daughter cells resulting from binary division share the parental protoplasm between them and the parent does not die but simply loses her identity in her offspring.

A process known as endomixis has been described in several species of PROTOZOA including *Paramæcium* (see page 79).

*Symbiosis.* — This term is used to imply the permanent association of two specifically distinct organisms so dependent on each other that life apart is impossible. Many PROTOZOA such as the ciliates *Paramæcium bursaria* and *Stentor polymorphus* and certain RADIOLARIA contain symbiotic algæ known as ZOOXANTHELLÆ. Some PROTOZOA are symbionts of higher organisms, for example, flagellates in the intestine of termites (page 52).

*Protozoa of the soil.* — That PROTOZOA live in the soil is not generally realized. They appear, however, to be present in all soils, being most abundant at a depth of six inches and few in number at depths of from some twelve to eighteen inches. About 250 species have been recorded from soil; most of these occur in fresh

water also. The types most commonly encountered in order of abundance are small flagellates, amœbæ, thecamœbæ, and ciliates. Some of the common genera are the flagellates, *Cercomonas*, *Oikomonas*, *Heteromita*, and *Spiromonas*; the SARCODINA, *Naegleria*, *Hartmanella*, *Amœba*, and *Diffugia*; and the ciliates, *Enchelys*, *Colpidium Colpoda*, and *Gonostomum*. The number of PROTOZOA in the soil depends chiefly on the size of the soil particles and the amount of organic material present. Cutler reports in ten samples of soil, five from a manured plot and five from one that had not been manured for many years, 1690 amœbæ, 7460 flagellates, and 15 ciliates per gram. There appears to be a definite relation between the number of PROTOZOA and bacteria present since the latter serve as food for the PROTOZOA. Soil PROTOZOA multiply readily in a medium rich in organic matter, such as a hay infusion, and can easily be cultivated in the laboratory by adding a few grams of soil to such a medium in a covered dish.

The history of our knowledge of Protozoa. — PROTOZOA were unknown before microscopes were invented. They were first seen and described by Anton von Leeuwenhoek (1632-1723). About thirty species described by him are recognizable to-day. The first one was a *Vorticella* described in 1675. Later in 1681 he found in his own stools and described the first protozoon from man, now known as *Giardia lamblia*. Protozoa soon became favorite material for study and played a prominent rôle in the development of biology, but only a few names and discoveries can be included here. Joblot (1718) showed that no PROTOZOA appeared in a hay infusion unless exposed to the atmosphere, thus disproving the theory of the spontaneous generation of PROTOZOA. He likewise (1754) discovered the contractile vacuole and the importance of the arrangement of cilia. Spallanzani (1729-1799) also disproved the spontaneous generation of PROTOZOA by demonstrating that they do not develop in a vacuum and hence must come from the air. Part of the life history of the vorticellas was worked out by Trembley (1747). The nature of the PROTOZOA was being discussed at this time and was not conceded by Linnæus to be of the animal type until 1767. Order was established for the PROTOZOA by O. F. Müller (1786), who adopted binomial nomenclature and named nearly 400 species, of which 150 remain in the group to-day. The term INFUSORIA was applied to the entire phylum. Ehrenberg's large monograph on *The Infusoria*,

as *Complete Organisms* appeared in 1836. He, like many other investigators at this time, believed PROTOZOA to possess eyes and various internal organs characteristic of higher animals. The SARCODINA were studied particularly by Dujardin (1801-1860) who called their protoplasm "sarcode." The term protoplasm was applied to the cell substance by Purkinje in 1840 and by von Mohl in 1846. The unicellular nature of the PROTOZOA was established by von Siebold in 1848.

From this time on many students of the PROTOZOA advanced our knowledge of the phylum and published large monographs on the various types; among these should be mentioned those of Stein, Bütschli, Leidy, Doflein, Kofoed, and Wenyon. Parasitic PROTOZOA did not attract particular attention until it was discovered that certain species were pathogenic to lower animals or to man. The discovery of each new pathogenic species has been followed by a flood of literature representing the results of investigation by many students. Among the disease-producing parasitic PROTOZOA of man should be mentioned *Endamæba histolytica* of amœbic dysentery and amœbic liver abscess, the trypanosomes of African sleeping sickness and of Chagas' disease in South America, the leishmanias of oriental sore and kala-azar, the intestinal flagellates, *Balantidium coli* of ciliate dysentery, and the malarial parasites. Important agents of animal diseases are the trypanosomes of dourine, nagana, surra, mal-de-caderas, and murrina in cattle, horses, and mules, the coccidia of birds and rabbits and the piroplasmas of Texas fever in cattle and other similar diseases.

**Protozoa and Metazoa.** — It is usually assumed by zoologists that METAZOA have evolved from PROTOZOA, and, granted the truth of evolution, the assumption that the many-celled animals developed from protozoan-like ancestors seems reasonable. How this took place during the remote ages in the history of life upon the earth is a difficult and unsolved problem. Among PROTOZOA, as already described, are species consisting of many cells forming colonies in some of which the cells have become differentiated into somatic cells and germ cells. In certain species the somatic cells are of several types which perform different functions. Such an organism is really a metazoon. It is impossible to state definitely, however, that the METAZOA have evolved by the aggregation of similar cells into colonies and their subsequent differentiation although this seems quite probable. The possibility

has also been suggested that the METAZOA have arisen from multinucleate PROTOZOA in which each nucleus assumed control of that portion of the cytoplasm immediately surrounding it and the so-called energids thus formed developed different functions.

**Classification of the Protozoa.** — No classification of the PROTOZOA has been adopted by all protozoologists. The one presented here is much abbreviated and arranged so as to be of use to one who is not specializing in protozoology. It includes particularly those groups that are most frequently encountered by zoologists.

**PHYLUM PROTOZOA.** — Unicellular animals.

**CLASS I. SARCODINA.** — With pseudopodia.

**SUBCLASS I. RHIZOPODA.** — Typically creeping forms with lobose (branched, root-like or finger-like) or reticulose (anastomosing) pseudopodia.

**Order 1. LOBOSA.** — Amœboid forms of simple structure and lobose pseudopodia; skeleton lacking or in form of a simple shell.

**Suborder 1. GYMNAMOEBA.** — Without shell or skeleton.

**Suborder 2. THECAMOEBA.** — With shell.

**Order 2. PROTEOMYXA.** — With filose or reticulose pseudopodia and without shells. Flagellated and heliozoon-like stages often occur.

**Order 3. FORAMINIFERA.** — With reticulose pseudopodia and with shells.

**SUBCLASS II. ACTINOPODA.** — Typically floating forms with radiating, unbranched pseudopodia.

**Order 4. HELIOZOA.** — Principally fresh water, without a "central capsule."

**Order 5. RADIOLARIA.** — Exclusively marine, with a "central capsule."

**CLASS II. MASTIGOPHORA.** — With flagella.

**SUBCLASS I. PHYTOMASTIGINA.** — Plant-like flagellates.

**Order 1. CHRYSOMONADIDA.** — Holozoic or holophytic. One or two yellowish chromatophores; 1-2 flagella; with or without stigmata.

**Order 2. CRYPTOMONADIDA.** — Holophytic or saprophytic. Two flagella associated with canal and contractile vacuole; 2 chromatophores may be present.

**Order 3. DINOFLAGELLIDA.** — Holozoic or holophytic. Most forms have a thickened cuticle which forms a



lorica. Two flagella which usually lie in two grooves in the lorica, the longitudinal one in the longitudinal groove or sulcus, and the transverse one in the circular groove or girdle.

**Order 4. PHYTOMONADIDA.** — Exclusively holophytic. Body covered with cellulose wall and without mouth opening.

**Order 5. EUGLENOIDIDA.** — Holozoic, holophytic, or saprophytic. One or two flagella associated with mouth aperture and canal; complex vacuole system opening into canal; often contains chromatophores, stigmata, etc.

**SUBCLASS II. ZOOMASTIGINA.** — Animal-like flagellates.

**Order 6. PANTASTOMIDA.** — Holozoic; no mouth opening; food ingested by means of pseudopodia anywhere on body surface.

**Order 7. PROTOMONADIDA.** — Holozoic, saprophytic, or entozoic. In first case food ingested at a definite place on body (generally at base of flagellum) where a permanent mouth opening may be present or absent. Flagella 1-2.

**Order 8. POLYMASTIGIDA.** — Mostly entozoic; body in some bilaterally symmetrical; 3-8 flagella.

**Order 9. HYPERMASTIGIDA.** — All entozoic in gut of insects. Flagella very numerous and generally arranged as a thick bunch at anterior end of body.

**CLASS III. SPOROZOA.** — No locomotor organelles. All parasitic.

**SUBCLASS I. TELOSPORIDIA.** — Formation of spores by adults, ending life of the parent.

**Order 1. GREGARINIDA.** — Cœlozoic; reproduction usually by sporogony only.

**Order 2. COCCIDIA.** — Cytozoic, alternation of schizogony and sporogony.

**Order 3. HÆMOSPORIDIA.** — Cytozoic in blood cells of vertebrates; alternation of schizogony and sporogony in alternate hosts; usually no resistant spores.

**SUBCLASS II. CNIDOSPORIDIA.** — Formation of spores during growth of parent.

**Order 1. MYXOSPORIDIA.** — Large multinucleate plasmodium; large spores with usually two polar capsules.

- Order 2. MICROSPORIDIA.** — Spores very small with usually one polar capsule.
- SUBCLASS III. ACNIDOSPORIDIA.** — Spores without polar capsules.
  - Order 1. SARCOSPORIDIA.** — Parasites in muscle cells of vertebrates forming sack-like spore cases (Miescher's tubules).
  - Order 2. HAPLOSPORIDIA.** — Parasites mostly of fish and invertebrates.
- CLASS IV. INFUSORIA.** — With cilia.
  - SUBCLASS I. CILIATA.** — With cilia throughout life.
    - Order 1. HOLOTRICHIDA.** — Cilia uniformly distributed over entire body.
    - Order 2. HETEROTRICHIDA.** — Cilia or membranelles forming adoral zone. Generally of swimming habit, sometimes sedentary.
    - Order 3. HYPOTRICHIDA.** — Typically creeping; body flattened, with dorsal and ventral surfaces; usually with cirri on ventral surface.
    - Order 4. PERITRICHIDA.** — Typically sedentary; spiral runs down into mouth.
  - SUBCLASS II. SUCTORIA.** — Adult organisms sedentary and devoid of cilia; larval stages free-swimming and ciliated.

## 6. REFERENCES TO LITERATURE ON THE PROTOZOA

The references listed below are for the most part books. In these books will be found extensive bibliographies to the literature on PROTOZOA contained in scientific journals and monographs. Current literature can best be obtained from journals that often include papers on PROTOZOA and from bibliographies. Among the former are the *Biological Bulletin*, *Journal of Experimental Zoology*, *American Journal of Hygiene*, *Archiv für Protistenkunde*, *Journal of Parasitology*, and *Parasitology*. The bibliographies of most use are the *Zoological Record*, *Biological Abstracts*, *Quarterly Cumulative Index Medicus*, and *Tropical Diseases Bulletin*.

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## CHAPTER II

### PHYLUM PORIFERA

#### INTRODUCTION

The study of sponges is often omitted from introductory courses in zoology because these animals seem to be the remnants of a group that separated from the other METAZOA at an early stage in the evolutionary series of animals and have remained in their primitive condition ever since. For this reason the METAZOA are sometimes arranged in two groups, one containing the sponges

and designated the PARAZOA and the other the METAZOA proper.

Most sponges are marine but a few live in fresh water. The bath sponges that are familiar to all of us consist of the skeleton of certain PORIFERA that live in the sea.

Sponges are usually attached and stationary animals in the adult stage, distribution being brought about largely by the actively swimming ciliated larvæ or by currents of water which carry the young from place to

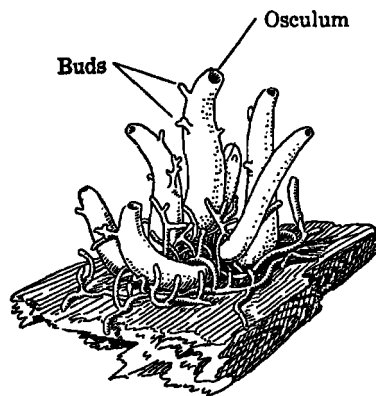


FIG. 77. — *Leucosolenia*. A small colony. (From Woodruff.)

place before they become attached. The thousands of different species vary greatly in shape, size, structure, and geographical distribution. They were for centuries considered to be plants and their animal nature was not established until about 1857.

Sponges are not easy to classify but are usually arranged in three classes as follows:

CLASS I. CALCAREA (Lat. *calcarius*, lime), with spicules of carbonate of lime.

CLASS II. HEXACTINELLIDA (Gr. *hex*, six: *aktin*, ray), with triaxon spicules of silicon.

CLASS III. DEMOSPONGIA (Gr. *demos*, people; *spongos*, sponge), usually with spicules of silicon, not triaxon, or with spongin, or with both spicules and spongin.

# 1. CLASS I. CALCAREA

## (1) LEUCOSOLENIA

*Leucosolenia* (Fig. 77) is a sponge which will serve to illustrate the structure of the most simple members of the phylum. It is found growing on the rocks near the seashore just below low-tide mark, and consists of a number of horizontal tubes from which branches extend up into the water. These branches have an opening, the *osculum*, at the distal end, and *buds* and *branches* projecting from their sides. The buds and branches are hollow, possessing a single *gastral cavity* which communicates with the horizontal tubes. The entire mass is a colony of animals, and the tissues connected with a single osculum may be considered an individual sponge.

If a branch is examined under a microscope, it will be found to contain a large number of three-pronged (triradial) *spicules*, which are embedded in the soft tissues of the body wall (Fig. 78); these serve to strengthen the

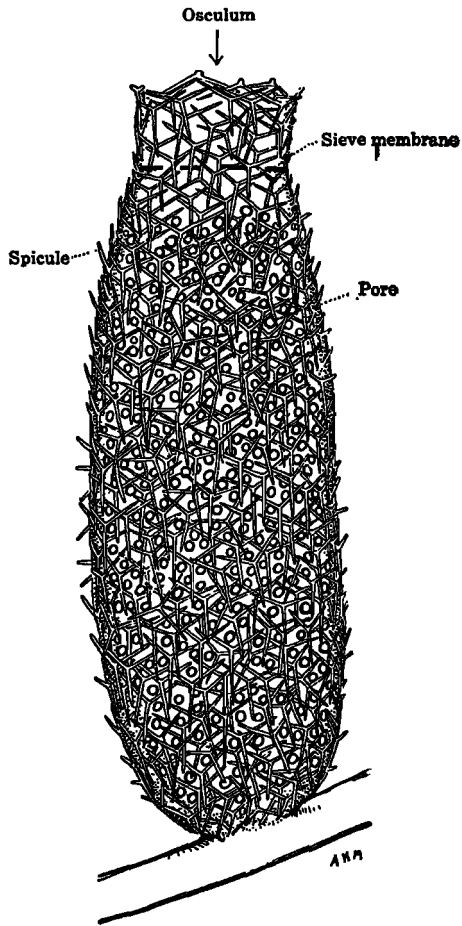


FIG. 78. — A young ascon sponge; (From Kerr.)

body and hold it upright. The application of acid results in the dissolution of these spicules and the production of an effervescence, thus proving them to be composed of calcium carbonate. The body wall is so flimsy that it is difficult to study even under the best conditions. It is made up of two layers of cells (Fig. 79): an outer layer, the *dermal epithelium*, and an inner layer, the *gastral epithelium*. These layers, as will be shown later are not comparable to the ectoderm and endoderm of the COELENTERATA and other METAZOA. Between these two layers is a jelly-like substance similar to the mesoglea of *Hydra* in which are many *amœba-like wandering cells*.

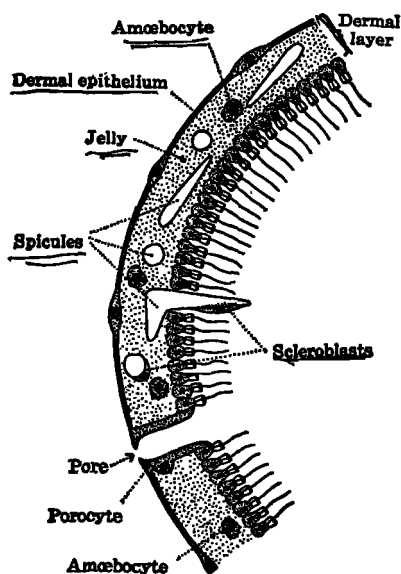


FIG. 79. — Structure of body wall of an ascon sponge. (From Kerr.)

The gastral epithelium is peculiar, since it consists of a single layer of *collar cells*, the *choanocytes* (Fig. 79), which resemble the similar cells of the choanoflagellate PROTOZOA (Fig. 35, b). The flagella of these collar cells beat constantly, creating a current of water.

If a little coloring matter is placed in the water, it will be drawn into the animal through minute *incurrent pores*, the *ostia* (Fig. 79), in the body wall and will pass out through the openings in a sieve-like membrane stretched across the osculum

(Fig. 78). The osculum is therefore the *exhalant opening*, and not the mouth, as a casual examination might lead one to believe. The course of the current of water in such a sponge is shown by arrows in figure 92, A. The presence of the incurrent pores suggested the name PORIFERA for members of this phylum.

## (2) GRANTIA

*Grantia* (Fig. 80) is a simple sponge inhabiting the salt water along the coast of the New England states just below the low-tide mark. Here it is found *permanently* attached by one end to rocks

and other solid objects. Its distribution in space is effected during the early embryonic stages, at which time cilia are present, enabling it to swim about.

**Morphology.** — *Grantia* varies in length from one half an inch to almost an inch, and resembles in shape a slender vase that bulges slightly near the center. The distal end of the animal opens to the exterior by a large *excurrent pore*, the *osculum*. This opening is surrounded on all sides by a circlet of long straight needles called *spicules*. Smaller spicules protrude from other parts of the body, giving the animal a ciliated appearance. The body wall is perforated by numerous *incurrent pores*.

A specimen of *Grantia* split longitudinally (Fig. 80) shows the body to be a hollow sac, one large central gastral cavity, the *cloaca*, being present. The body wall is honeycombed by a great many canals; some of these, the *radial canals*, open to the gastral cavity through minute pores, the *apopyles*, and end blindly near the outer surface; others, the *incurrent canals*, open to the outside through small incurrent pores or *ostia*, and end blindly near the inner surface of the body wall; still other canals, the *prosopyles*, even smaller than those already noted, connect the radial with the incurrent canal. Figure 80 shows in longitudinal section the gastral cavity of a simple sponge, in the sides of which are the openings of the radial canals; the body wall is seen to be crowded with both radial and incurrent canals, which have been cut lengthwise. The relations of the various canals to one another are shown in figure 92, *B*; here the arrows indicate the direction of the current of water, which enters the incurrent canal, passes through the prosopyles into the radial canal, and thence into the gastral cavity, finally escaping from the body by way of the osculum. The surface area of the epithelium covering the body, and lining the internal cavities, is enormously increased by the canal system.

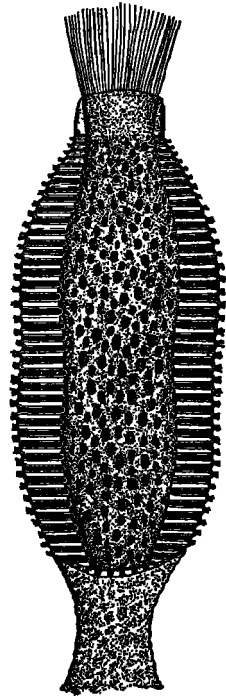


FIG. 80. — Diagram of a sycon sponge, such as *Grantia*, slit open longitudinally. (From Borradaile and Potts.)



*Grantia* is an animal possessing an outer dermal layer of cells, an inner gastral epithelium, and a middle region containing cells of several varieties (Fig. 81). The *dermal epithelium* covers the entire outer surface of the body, and lines the incurrent canals. It is composed externally of a single layer of flat cells. Wherever prosopyles occur connecting the incurrent with the radial canals,

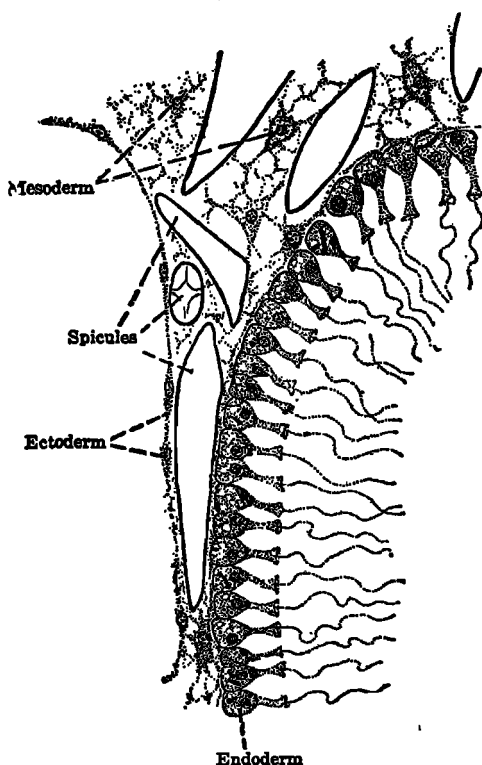


FIG. 81. — *Grantia*. Part of body wall.  
(From Dahlgren and Kepner.)

a single large dermal cell, termed a porocyte, is present. The *porocytes* are derived from cells of the dermal epithelium. They are large and granular, and frequently exhibit amoeboid movements. The prosopyle is an intracellular perforation of the porocyte. Cells, called *scleroblasts*, which produce spicules, are also considered constituents of the dermal layer.

The *inner epithelium* lines the cloacal cavity and the radial canals. In the latter it consists of one layer of collared flagellated cells (Fig. 81), the *choanocytes*. The collar of these cells consists of from 20 to 30 parallel rods fused

side by side and capable of contraction. No collar cells are present in the epithelium lining the cloacal cavity. The flagella of the collar cells create the current of water which is continually flowing through the body wall into the cloacal cavity and out of the osculum.

The *middle region* of the body wall is not so definite nor firm in structure as are the outer and inner epithelia, but, neverthe-

less, it is considered a distinct cellular layer. *Amœboid wandering cells*, which ingest food or act as storage cells, are found here, as well as the *reproductive cells* which always arise in the middle layer.

The soft body wall of *Grantia* is supported and protected by a skeleton composed of a great number of *spicules* of carbonate of lime. Four varieties of spicules are always present, (1) long straight monaxon rods guarding the osculum, (2) short straight monaxon rods surrounding the incurrent pores, (3) tri-radiate spicules always found embedded in the body wall, and (4) T-shaped spicules lining the gastral cavity; four- and five-rayed spicules may also be present. Spicules are built up within cells called *scleroblasts* (Fig. 82), which form part of the inner stratum of the dermal layer. A slender organic axial thread is first built up within the cell; around this is deposited the calcareous matter; the whole spicule is then insheathed by an envelope of organic matter like that composing the axial thread.

**Nutrition.**—*Grantia* lives upon the minute organisms and small particles of organic matter that are drawn into the incurrent canals by the current of water produced by the beating of the collar-cell flagella. Some of the food particles are probably ingested by the porocytes; but the majority of them are engulfed by the collar cells. *Digestion*, as in the *PROTOZOA*, is intracellular, food vacuoles being formed. The distribution of the nutriment is accomplished by the passage of digested food from cell to cell, aided by the amœboid wandering cells of the middle layer.

*Excretory matter* is discharged through the general body surface, assisted probably by the amœboid wandering cells, and possibly by the collar cells also. *Respiration* likewise takes place, in the absence of special organs, through the cells of the body wall.

Sponges do not possess differentiated *nervous organs*, but are able to respond to certain stimuli. The pores and *oscula* are surrounded by contractile cells, called *myocytes*, which are able to close these openings. Apparently these cells respond to direct stimulation, since no nervous tissue is present. They, therefore,

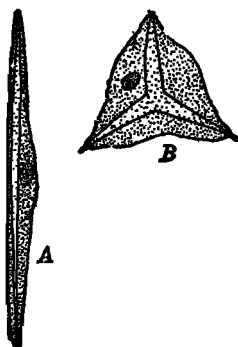


FIG. 82. — Developing spicules of a sponge. (From Dahlgren and Kepner.)

represent what may be considered the very beginning of a neuromuscular mechanism.

**Reproduction.** — Reproduction in *Grantia* takes place by both sexual and asexual methods. In the latter case, a *bud* arises near the point of attachment, finally becomes free, and takes up a separate existence.

The *sexual reproductive cells* lie in the middle layer of the body wall. Both eggs and sperms occur in a single individual *i.e.* *Grantia* is *monœcious* or *hermaphroditic*. *Spermatogenesis* is probably similar to that of an allied genus, *Sycon*. The primordial germ cell, called a spermatogonium, divides, producing a covering cell, the spermatocyst, and a central sperm mother cell, the spermatocyte. The latter forms a number of spermatids by mitosis; these transform into spermatozoa. The *ova* arise by the growth of certain cells of the middle layer which are nourished by neighboring cells. In *Sycon*, two polar bodies are formed; the sperm penetrates the egg just before the formation of the second polar body.

**Embryology** (Fig. 83). — The development of the fertilized egg has been observed in *Sycon* and is probably similar to what occurs in *Grantia*. The egg segments by three vertical divisions into a pyramidal plate of eight cells. A horizontal division now cuts off a small cell from the top of each of the eight, the result being a layer of eight large cells crowned by a layer of eight small cells. The cells now become arranged about a central cavity, producing a *blastula-like sphere*. The small cells multiply rapidly and develop flagella, while the large cells become granular. The small cells are now partially grown over by the others, forming a structure called the *amphiblastula*. The mass of cells then becomes disk-shaped by the pushing in of the flagellated cells. Two layers are thus formed, between which the middle layer arises. The invaginated side soon becomes attached, and the embryo lengthens into a cylinder at the distal end of which an opening, the osculum, appears. In the meantime, spicules and the canal system arise in the body wall.

## 2. OTHER PORIFERA

**CLASS I. CALCAREA.** — The CALCAREA are all marine and live in shallow water. They are comparatively simple in structure. Two orders and about 150 species are known. As their name indicates their chief characteristic is the presence of calcareous spicules.

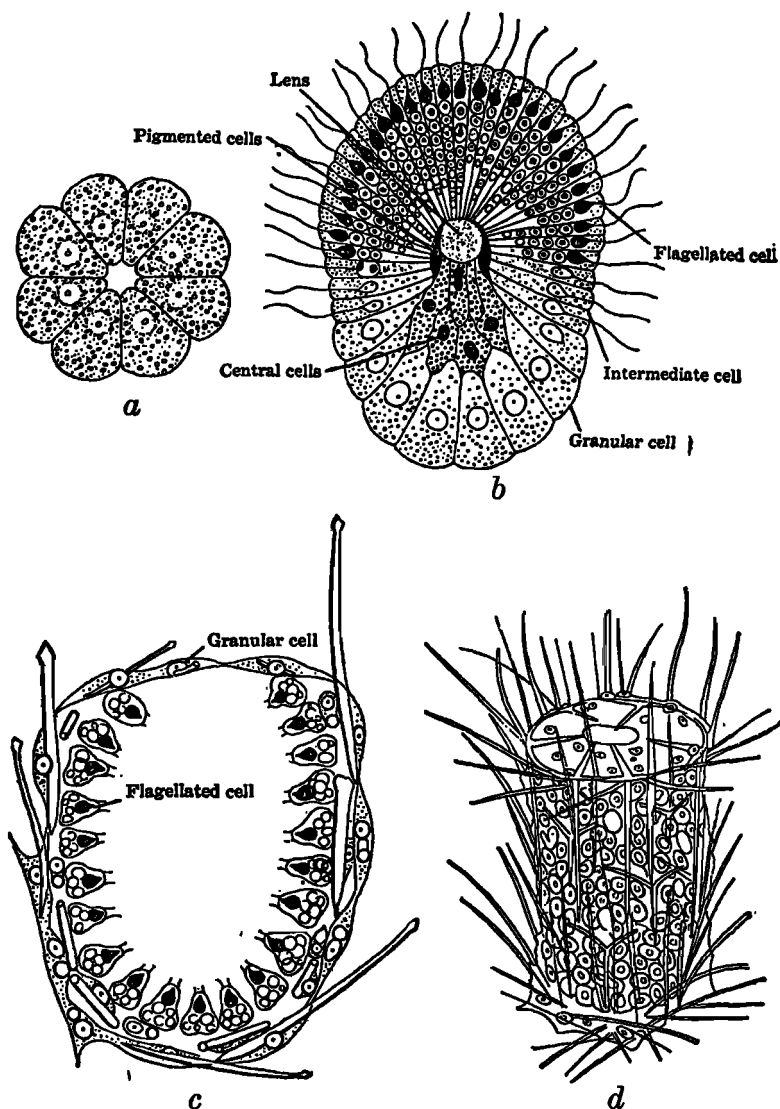


FIG. 83. — Embryology of sponges. a, An egg of *Sycandra* that has reached the 8-cell stage. b, An amphiblastula larva of *Leucosolenia*. c, Young *Leucosolenia* four days old. d, Older stage in *Sycon rdphanus*. (a, d, after Schulze; b, c, after Minchin.)

**Order 1. HOMOCÆLA.** — The 50 species in this order are the simplest of all sponges and may be separated into two families, the LEUCOSOLENIIDÆ and the CLATHRINIDÆ (Fig. 84). The characteristics of the order have been presented by *Leucosolenia* as a type. The body wall is thin; the gastral cavity is lined with collar cells and each pore is a perforation in a single cell.

**Order 2. HETEROCÆLA** (Fig. 84). — *Grantia* has served to introduce this order consisting of six families and about one hundred species. The body wall is thickened; the cloacal cavity is lined with flattened epithelial cells and the collar cells are located in radial canals or

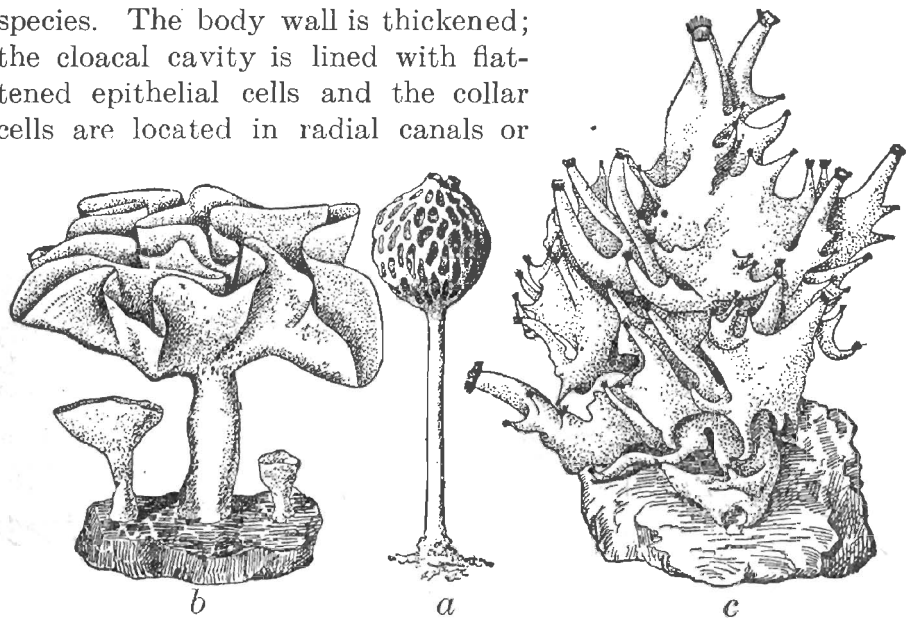


FIG. 84. — Types of sponges. a, HOMOCÆLA. *Clathrina lacunosa*. b, HETEROCÆLA. *Grantia labyrinthica*; three stages of growth. c, HETEROCÆLA. *Leucandra aspera*. (a, c, after Minchin; b, after Dendy.)

chambers. *Grantia ciliata* occurs from Rhode Island to Greenland; *Leucandra taylora* lives off the shore of Vancouver Island and *Amphoriscus thompsoni* in the Gulf of St. Lawrence.

**CLASS II. HEXACTINELLIDA.** — To this class belong the glass sponges. They are mostly deep-sea inhabitants and widely distributed. Their fossil remains are abundant and indicate that they have always been present in large numbers. They are characterized by the possession of siliceous spicules of the triaxon type, that is, with six rays or a multiple of six. The body is often tubular or basket-shaped and the spicules may form a continuous skeleton resembling spun glass. Venus' flower basket, *Euplectella aspergillum* (Fig. 85), is especially abundant near the Philippine Islands:

its skeleton is often seen in museums. It has a long, curved, cylindrical body held up by a framework of spicules. In nature it is fastened in the mud of the sea bottom by a mass of long siliceous threads at the posterior end. The body wall, as in all HEXACTINELLIDA, contains simple thimble-shaped flagellated chambers. The large cloacal cavity often serves as a residence for a pair of decapod crustaceans, *Spongicola venusta*. *Euplectella suberea* occurs in the West Indies. Another American hexactinellid is *Hyalonema longissimum* (Fig. 86) which lives off the New England coast at depths of from 60 to 95 fathoms.

### CLASS III. DEMOSPONGIA. —

These are the dominant PORIFERA of the present time being widespread in nature and very numerous in species and individuals. Most of the sponges that are generally seen belong to this class. They are often massive and brightly colored,

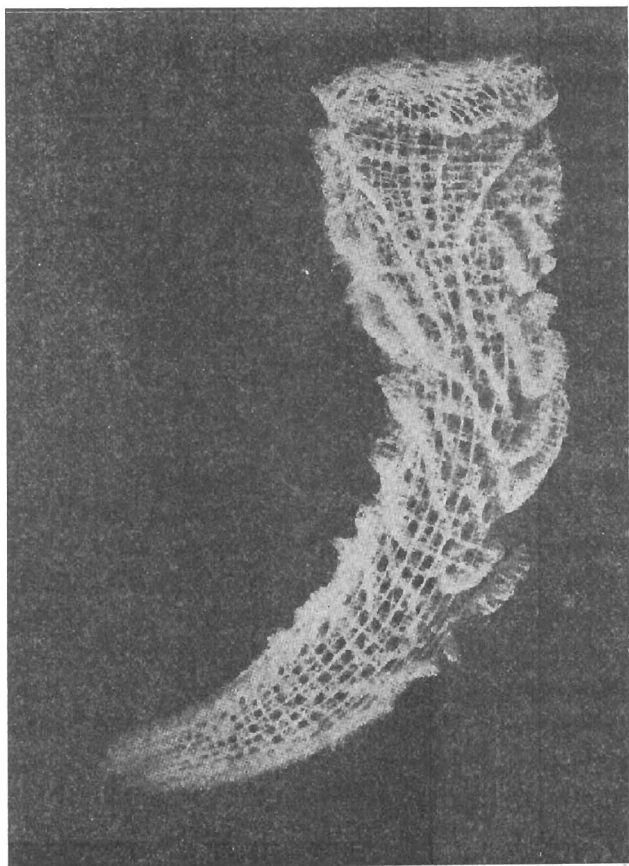


FIG. 85. — HEXACTINELLIDA. *Euplectella aspergilum*: siliceous skeleton known as Venus' flower basket. (From Kerr.)

with complicated canal systems connected with small spherical flagellated chambers. The skeleton may consist of siliceous spicules, but these are not triaxon as in the HEXACTINELLIDA. Spongin, a substance related to silk, may provide all of the skeleton or be combined with siliceous spicules. Some spicules are straight and needle-shaped (monaxon); others have eight rays (tetraxon).

**Order 1. TETRAxonIDA** (Fig. 87). — Sponges belonging to this order live mostly at depths of 50 to 200 fathoms and are usually attached to the bottom by tufts of spicules. The outer, dermal layer of the body, the cortex, is thickened and contains skeletal spicules, megascleres, which unite to form the supporting framework. Other spicules, microscleres, lie scattered in the mesoglea. These spicules are modifications of the tetraxon type. Among the members of

this order from America are *Thenea echinata*, which occurs on the New England coast north of Cape Cod and is shaped like a mushroom; and *Geodia mülleri*, which is found in the West Indies and is irregularly lobed.

**Order 2. MONAXONIDA** (Figs. 88, 89). — This order contains most of the living species of sponges. They usually inhabit shallow water including one family in fresh water. Their spicules are of the monaxon type. Spongin may be present. In one of the two subor-

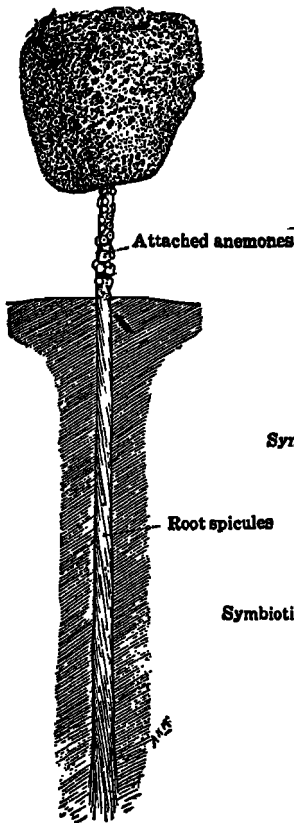


FIG. 86. — HEXACTINELLIDA: *Hyalonema*. (From Kerr.)

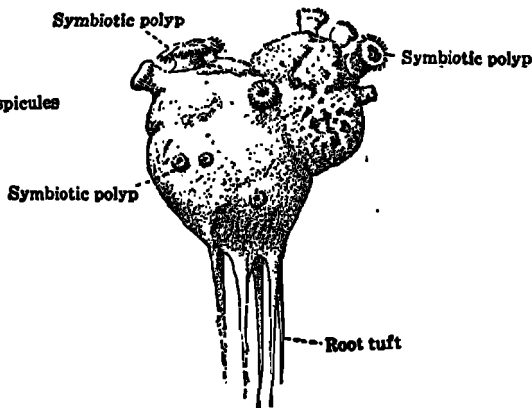


FIG. 87. — DEMOSPONGIA. *Thenea muricata*, an example of the order TETRAxonIDA. (After Minchin.)

ders there is a hard, outer cortex which is absent from the other suborder. *Suberites compacta* is an American species that ranges from Virginia to Maine. It has a bright yellow, elongated

body that may reach a length of 15 cm. and is often attached by one edge to the shells of hermit crabs. Another species with a similar range is *Polymastia robusta*. This is a yellowish or grayish species of irregular form with finger-like branches. It reaches a diameter of 30 cm. *Cliona celata*, the sulphur sponge, occurs along our eastern coast. It is bright yellow in color and may form a mass up to 20 cm. in diameter. The young clionas are able to bore their way into calcareous rocks or the shells of mollusks forming tunnels in which they live. *Chalina oculata* (Fig. 88) is the finger sponge, so named because of its being shaped like a hand with many fingers. The skeleton is of spongin in which siliceous spicules are embedded. It is orange or red in color and is common from Rhode Island to Labrador. *Microciona prolifera* is a bright red species that forms digitate masses up to 51 cm. in height on shells and stones and is abundant in Long Island Sound. *Esperella fibrezilis* occurs on the docks at Woods Hole, Mass. It is yellowish-brown in color and irregular in shape and may be covered with hydroids and algæ.

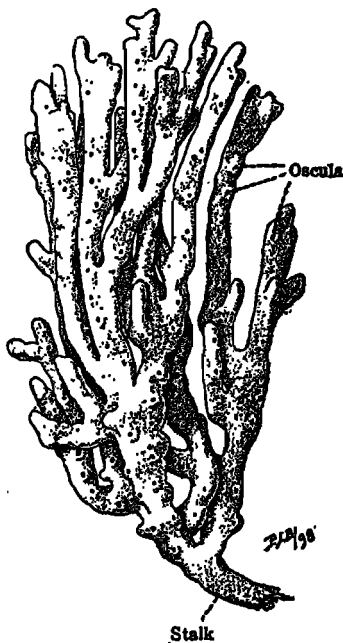


FIG. 88. — DEMOSPONGIA. *Chalina oculata*, an example of the order MONAXONIDA. (After Minchin.)

**Fresh-water sponges.** — These belong to the family SPONGILLIDÆ in the order MONAXONIDA. They are usually to be found in clear water encrusting stones, sticks, and plants; but may also occur on the soft mud bottom and in highly colored water and even in waters contaminated by industrial and organic wastes. Fresh-water sponges are usually yellow, brown, or green in color. The green color is due to the presence of ZOOCHLORELLÆ. These sponges reproduce by the formation of gemmules and the characteristics of these gemmules are the chief means of identification. More than twenty species occur in this country. Some of the more



common are as follows. *Spongilla lacustris* (Fig. 90) is the most abundant species. It prefers running water; is a branching form that lives in sunlight; and is usually green in color. *S. fragilis* is also a common species, but prefers standing water and avoids the light. *Ephydatia mülleri* is cushion-shaped and rarely branched. It is usually yellow or brown in color and prefers standing water. *Heteromeyenia ryderi* lives in shallow

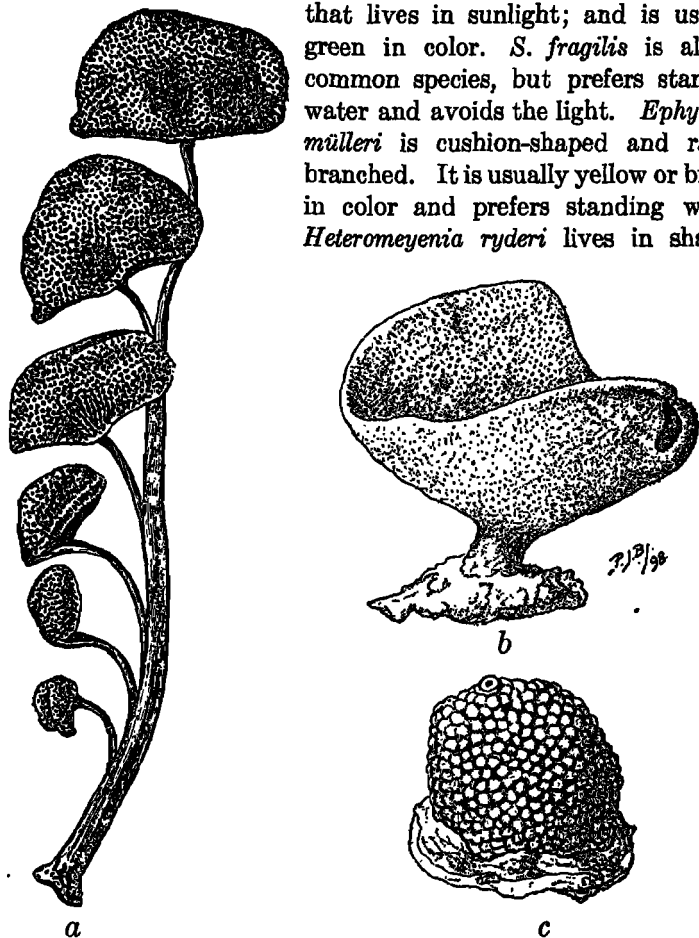


FIG. 89. — DEMOSPONGIA of the order MONAXONIDA. a, *Esperiopsis challengeri*. b, *Phakellia ventilabrum*. c, *Telhya lyncurium*. (a, after Ridley, from Minchin; b, c, after Minchin.)

flowing water; is light green in color and massive in type. *Tubella pennsylvanica* lives in shallow water; is gray or green in color and only about 6 mm. in diameter. It is averse to light and lives usually under stones and roots. *Carterius tenosperma* is an irregularly-shaped sponge, yellowish-green in color, that

encrusts plants, roots, and stones. It occurs in the eastern United States.

**Order 3. CERATOSA.**—Everyone is familiar with the skeletons of certain members of this order since the commercial sponges belong to this group. They occur in tropical and subtropical seas and are characterized by a skeleton of spongin. About a dozen species of these horny sponges are used by man. These belong to the genera *Euspongia*, *Hippospongia*, and *Coscinoderma*. The best sponges come from the Mediterranean and belong to the species *Euspongia officinalis mollissima* (Fig. 91) and *E. o. adriatica*. The glove sponge, *E. tubulifera*, is an American species of little commercial value.

**Order 4. MYXOSPONGIA** (Fig. 91). — Comparatively few sponges without any skeleton, and hence encrusting in habit, belong to this order. *Halisarca dujardini*, a slime sponge with elongate, sac-like flagellated chambers is an American species living on red algæ at a depth of about five fathoms off the coast of Rhode Island.

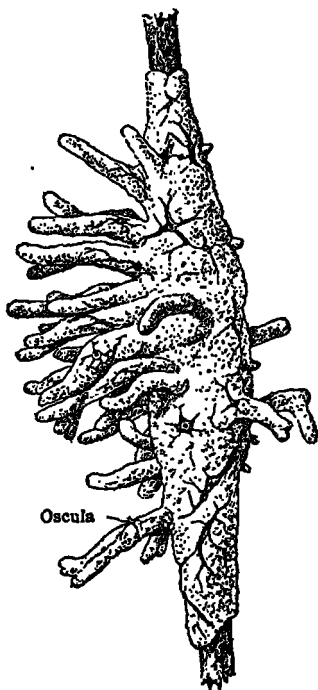


FIG. 90. — *Spongilla lacustris*, a fresh-water sponge. (After Weltner.)

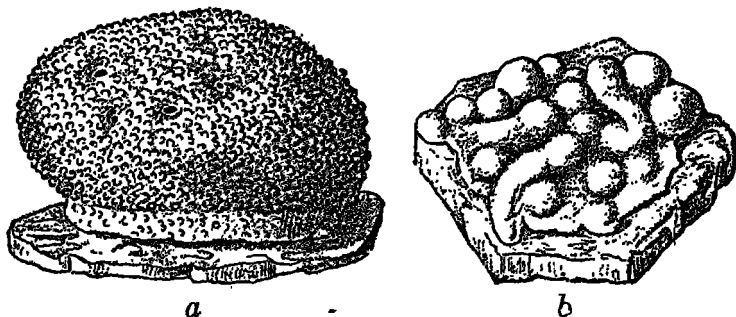


FIG. 91. — DEMOSPONGIA. a, CERATOSA. *Euspongia officinalis*, the bath sponge. b, MYXOSPONGIA. *Oscarella lobularis*. (After Schulze, from Minchin.)

## 3. SPONGES IN GENERAL

**External features.** — Sponges may be simple, thin-walled tubular structures like *Leucosolenia* and *Grantia*, or massive and more or less irregular in shape. Many sponges are indefinite masses of tissue encrusting the stones, shells, sticks, or plants to which

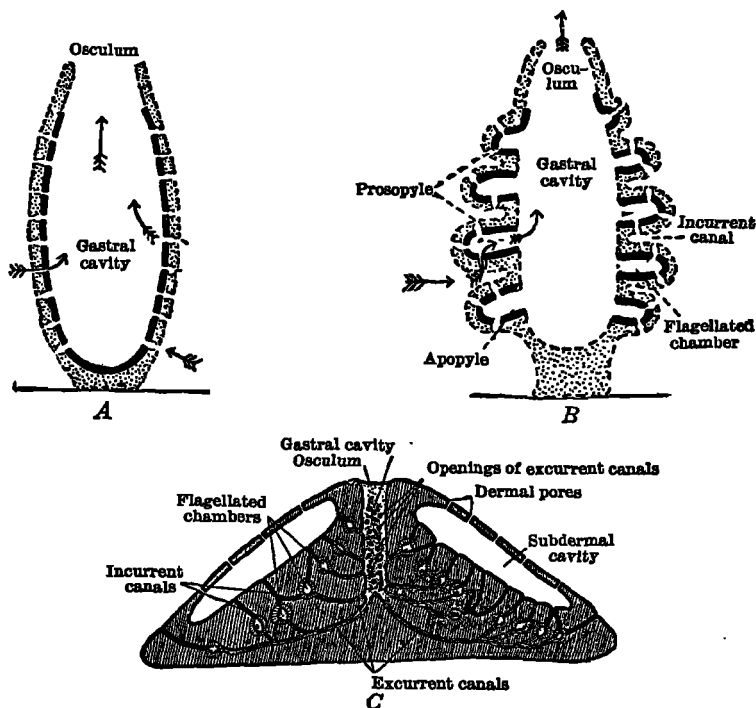


FIG. 92. — Sponges: types of canal systems. A, *ascon* type. B, *sycon* type. C, *rhagon* type (*Spongilla*). The arrows indicate the direction of the current of water. The thick black line in A and B represent the gastral layer; the dotted portion, the dermal layer. (A and B, from Minchin; C, from Parker and Haswell.)

they are attached; others are more regular in shape and attached to the sea bottom by means of masses of spicules. The form exhibited by the members of each species may vary somewhat but is nevertheless constant. Some are branched like trees; others are shaped like a glove, or a cup, or a dome. Sponges vary in size from species no larger than a pinhead to species that attain a diameter of three feet and a thickness of twelve inches. Certain

sponges appear to be ciliated because of the spicules that protrude from the body. Many sponges are white or gray but others are colored yellow, orange, red, or green. Green sponges usually owe their color to the green symbiotic algæ, *ZOOCHLORELLÆ*, contained in them.

**Canal systems.** — If it were not for the development of elaborate canal systems sponges would have remained in the simple condition of *Leucosolenia* and would never have been able to become massive in size. The canal system serves much the same purposes as the circulatory system does in higher animals; it furnishes a highway for food through the body and for the transportation of excretory matter out of the body. Three types are usually recognized.

The ascon type (Fig. 92, *A*) consists of incurrent pores, a gastric cavity lined with collar cells, and an osculum.

The sycon type (Fig. 92, *B*) is more complicated; the water flows through the dermal pores (ostia) into the incurrent canals; then through the chamber pores (prosopyles) into radial canals lined with collar cells; from here it is propelled by the flagella of the choanocytes into the cloacal cavity, finally passing out through the osculum.

In the rhagon type (Fig. 92, *C*) there are three distinct parts, (1) the water passes through the dermal ostia and by way of incurrent canals reaches (2) a number of small chambers lined with choanocytes, thence it is carried through (3) an excurrent system to the cloacal cavity and finally out of the osculum.

**Skeletal systems.** — All sponges, except those belonging to the small order MYXOSPONGIA, are provided with a skeleton. This may consist of carbonate of lime or silicon in the form of spicules or of spongin in the form of fibers more or less closely united. Siliceous spicules are composed of opal, a form of hydrated silica similar to quartz in its chemical reactions. Spicules are of various types and hence of value in arranging sponges into groups. As already noted the spicules in the class CALCAREA are calcareous; those in the class HEXACTINELLIDA are of the triaxon type; and those in the class DEMOSPONGIA are not triaxon, some being straight and needle-shaped (monaxon) and others eight-rayed (tetraxon). In the DEMOSPONGIA, spongin may be present with or without spicules in addition. Spongin is a substance chemically allied to silk. It is secreted by flask-shaped cells called spongioblasts.

Spicules are deposited in cells called scleroblasts and more than one cell may take part in the formation of a single spicule. The

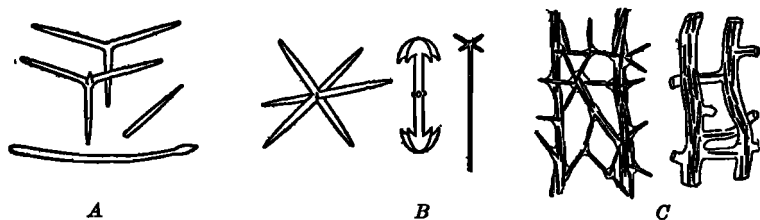


FIG. 93. — Spicules of sponges. A, calcareous spicules (*Leucosolenia*); B, siliceous spicules (*Hyalonema*); C, siliceous spicules with spongin (*Pachychalina* and *Chalina*). (From Kerr.)

carbonate of lime or silicon is, of course, extracted from the surrounding water by the cells. Some of the principal types of spicules are illustrated in figure 93. The arrangement of spongin fibers

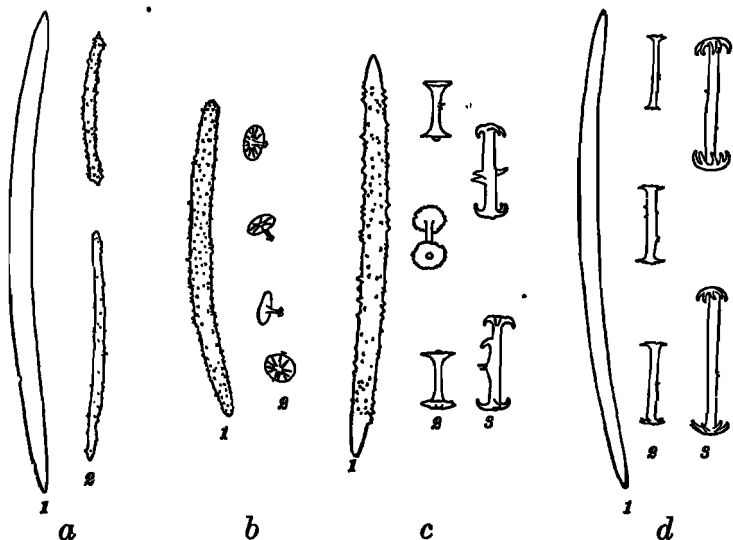


FIG. 94. — Spicules of fresh-water sponges. a, *Spongilla fragilis*, (1) skeleton spicule and (2) gemmule spicules. b, *Trochospongilla pennsylvanica*, (1) skeleton spicule, (2) gemmule spicules. c, *Heteromeyenia ryderi*, (1) skeleton spicules, (2) short gemmule spicules, (3) long gemmule spicules. d, *Heteromeyenia repens*, (1) skeleton spicule, (2) short gemmule spicules, (3) long gemmule spicules. (After Old.)

can be observed easily by placing a minute piece of a bath sponge under the microscope. Massive sponges could never have evolved

if it were not for spicules and spongin which form a skeleton that holds the body in shape preventing it from collapsing into a mass of jelly-like consistency in which canals and flagellated chambers could not possibly exist.

**Histology.** — Sponges are many-celled animals in which the somatic cells are differentiated into types for the performance of special functions; that is, division of labor among somatic cells has developed. This is a distinct and important advance over the condition existing even among such complex Protozoa as *Volvox*.

The cells of sponges may be separated into three groups: (1) those of the dermal layer, (2) those of the gastral layer, and (3) the amœboid cells in the jelly between the dermal and gastral layers. The classes of cells and the layers to which they belong are as follows:

A. Dermal layer	{	I. Epithelial stratum	{	1. Epithelial cells
				2. Contractile cells
				3. Gland cells
B. Gastral layer	{	II. Porocytes	{	4. Spongioblasts
				5. Pore cells
		III. Skeletogenous stratum		6. Scleroblasts
C. Middle region	{	IV. Gastral epithelium	{	7. Fiber cells
				8. Choanocytes
		V. Wandering cells		9. Ingestive cells
				10. Nutritive cells
				11. Storage cells
		VI. Reproductive cells		12. Gemmule cells
				13. Sexual cells

**Nutrition.** — Sponges obtain their food in the form of minute organic particles, living or lifeless, which enter the incurrent pores suspended in water, and are carried into the gastral cavity or flagellated chambers. The current of water flowing through the canal system of the sponge is created by the flagella of the choanocytes which beat continuously. The choanocytes also ingest the food particles either at the side or within the collar; a food vacuole is formed in which digestion takes place and the undigested residue is cast out from inside of the collar. The nutriment is passed from cell to cell and probably is circulated to a certain extent by the amœboid wandering cells of the middle layer. It

is necessary for the sponge to live in water that is circulating more or less, hence we find these animals in clear, not muddy water. Since the current of water passing through the sponge carries with it the excretions from the body, it is important that the water passing out of the osculum be forced away from the body, since it contains no more food particles but is loaded with carbonic acid and nitrogenous wastes poisonous to the sponge. Sponges are therefore so organized and so adapted to their environment that they are able to separate efficiently the water forced out of the osculum from that drawn in through the incurrent pores. This is accomplished by different species in different ways. The force and direction of the jet from the osculum is an important feature; also the nature of the currents at the bottom of the sea. It has been experimentally demonstrated that in *Stylotella* the pressure within the flagellated chambers is equivalent to a column of water 3.5 to 4.0 mm. in height. In another sponge, *Spinosella*, the osculum discharged about 0.9 c.mm. of water per second, or 78 liters per day. An average-sized specimen of *Spinosella* with 20 oscula would thus pass about 45 gallons of water through its canal system per day.

**Behavior.** — Sponges are comparatively inactive animals. The larvæ are ciliated and swim about but soon become attached to some solid object and remain fixed for life. At the time of fixation the young sponge may crawl for a short distance as a result of movements of the cells of attachment and thus reach a position where light and other conditions are more satisfactory. Thus, the young sponge that develops from a gemmule of *Spongilla* may crawl up the side of an aquarium. Certain adult sponges are capable of slight bending movements.

Activity is more pronounced within the body of sponges. This is due to the presence of contractile cells, the myocytes, which are arranged about the osculum and pores and in the wall of the canals in the form of sphincter-like bands. Stimuli of various sorts applied directly to these sphincters result in the opening and closing of the osculum, pores, and canals and in changes in the flow of water. Thus the osculum of *Stylotella* closes when the animal is transferred from moving into quiet water but opens when a current of water strikes it directly. Transmission to other oscula does not occur. There appears, however, to be present a sluggish type of transmission through the protoplasm, such as seems to

occur in certain PROTOZOA, to which the term neuroid has been applied. This is transmission without differentiated nervous elements such as are present in neural transmission. Studies of both the histology and behavior of sponges indicate that no true nervous elements exist. Sponges, therefore, have cells that act as effectors but no receptors or adjustors.

**Reproduction and growth.** — Reproduction in sponges is either asexual or sexual. By the asexual method there are produced buds and gemmules. Buds may be set free to take up a separate existence, or, as in *Leucosolenia*, may remain attached to the parent sponge. Often a complex assemblage of individuals is produced that may become very large.

Many marine and fresh-water sponges have a peculiar method of reproduction by the formation of gemmules. A number of cells in the middle layer of the body wall gather into a ball and become surrounded by a chitinous shell reinforced by spicules. In *Spongilla* the gemmules may possess a peripheral layer containing air cells that float them on the surface, and also rod-like spicules. These gemmules (Fig. 95) are formed during the summer and autumn. In the spring they develop into new sponges and are hence of value in carrying the race through a period of adverse conditions, such as the winter season. Young sponges that chance to become attached near together tend to coalesce.

In sexual reproduction the eggs and spermatozoa are derived as in *Sycon* from amoeboid wandering cells in the middle layer. A ciliated larva is produced from a holoblastic egg. This larva swims about for a while, thus effecting the dispersal of the species, then becomes fixed and passes through many changes, finally developing ostia and an osculum which are necessary for the nutritive processes and growth.

A peculiarity in the embryology of certain sponges is this: the flagellated cells of the larva do not become the outer (dermal) epithelium as do the flagellated cells of the larval coelenterate, but produce the gastral layer of choanocytes; and the inner cells do not become the inner (gastral) epithelium, as do the similarly situated cells in the coelenterate, but produce the dermal layer.



FIG. 95. — Gemmule of *Spongilla* in section showing thick wall, opening, and central mass of germinal cells. (From Weyssse.)



It, therefore, seems impossible to homologize the ectoderm and endoderm of cœlenterates and other METAZOA with the layers in the sponge larva, since the outer layer (ectoderm?) of the latter becomes the inner layer (endoderm?) of the adult sponge. The outer layer is consequently termed "dermal epithelium" instead of "ectoderm," and the inner, "gastral epithelium" instead of "endoderm."

The size and rate of growth of sponges depend on the species and largely on the nature of the environment. Annual sponges, that is, those that live one year or less are naturally smaller than perennials. Sponges may increase in weight as much as 40 per cent in a single day. Cuttings of bath sponges in Florida increased from  $2\frac{1}{2}$  cubic inches to  $12\frac{1}{2}$  cubic inches in two months. Certain commercial sponges, such as the wool sponges of the Caribbean Sea, grow to be  $2\frac{1}{2}$  feet in diameter and 25 years of age.

**Aggregates of sponge cells.** — Experiments with certain sponges (*Stylotella*, *Microciona*, etc.) prove that when a specimen is broken up and strained through fine bolting cloth so as to dissociate the cells, the cells will fuse on the bottom of a dish to form plasmodia. These plasmodia in the course of several months acquire canals, flagellated chambers, and a skeleton and develop reproductive bodies. The aggregation of these cells appears to be due to cells (archæocytes) from the middle layer which move about and gather in all the cells they encounter. When cells from two species are intermingled those of each species fuse with one another but not with those of the other species. These studies provide a remarkable case of what is known as regulation, whereby parts of an organism regain all of the characteristics of the species.

**Position of sponges in the animal kingdom.** — As already noted although sponges are undoubtedly multicellular animals, they are often separated from the METAZOA and placed in an isolated group, the PARAZOA, near the foot of the family tree. This is because they are supposed to have branched off from the main evolutionary series at this point and to have given rise to nothing but sponges. At any rate they do not appear to be closely related to any group of the METAZOA. They resemble, however, in certain respects some of the flagellated PROTOZOA, especially those with collar cells and colonial in habit, like *Proterospongia* (Fig. 96). This protozoon not only possesses choanocytes like those of sponges but cells within the colony that resemble those in the middle

layer of sponges. It is not difficult to imagine such an organism developing into a sponge.

**The relation of sponges to other animals and to man.** — Because of their habitat sponges are associated principally with aquatic animals. These seldom feed on sponges because of their skeletons of spicules and spongin and because of the distasteful ferments they excrete. A number of animals such as hydroids, sea-anemones,

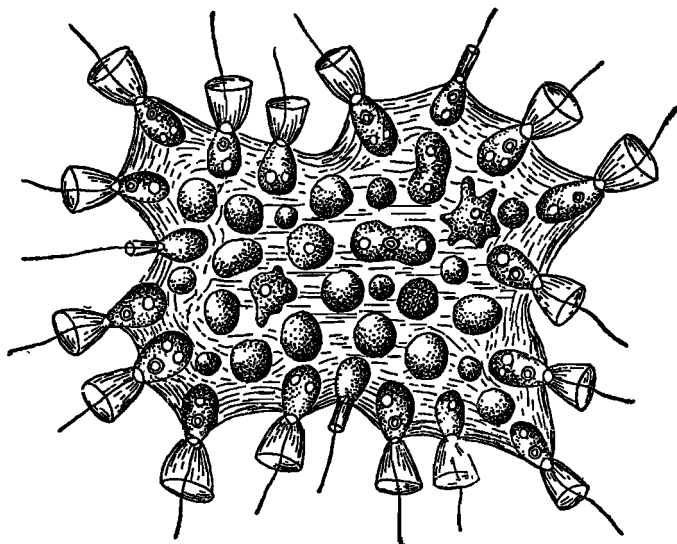


FIG. 96. — *Proterospongia haeckeli*. (After Kent.)

polychæte worms, ophiuroids, and crustaceans live, in more or less commensal or symbiotic relations, in the canals or cloaca of sponges.

Sponges are mostly beneficial to man. They may destroy oysters and other bivalves by covering their shells and depriving them of food; but, on the other hand, they supply us with the sponges of commerce, which are the spongin skeletons of certain species living chiefly near the shore of the Mediterranean Sea, and the coast of Australia, the Bahama Islands, Cuba, and Florida. Sponge culture, that is, the growing of sponges from cuttings, has been developed with some success.

**The history of our knowledge of Porifera.** — Although sponges have been recognized since at least the time of Aristotle (384–322 B.C.) they were not proved to be animals until 1857. Ellis in 1765 appears to have been the first to describe the current of

water entering and leaving a sponge. This was worked out more fully by Grant (1825) who observed the incurrent pores and oscula and suggested that the currents were due to ciliary action. After the recognition of the animal nature of sponges, their position in the animal kingdom became an important subject. The embryology of sponges as worked out by Schulze (1878), Bütschli (1884), Solas (1884), Minchin (1897), Maas (1898), and Delage (1898) indicated fundamental differences between them and other METAZOA which has led to their being considered a separate group and called PARAZOA.

**Classification.** — Sponges constitute a distinct phylum of animals. They are all multicellular and the somatic cells are arranged in two layers (diploblastic), an outer dermal and an inner gastral layer. The cells in these layers are further differentiated for various functions. The body is asymmetrical or radially symmetrical; it is perforated by incurrent pores usually opening into canals or chambers lined with flagellated collar cells (choanocytes), and is, in most species supported by a skeleton of spicules or spongin or both. The classes and orders are separated for the most part on the basis of the material composing the skeleton and the shape of the spicules.

**Class I. CALCAREA.** — Marine species, mostly white or gray, living in shallow water; spicules of carbonate of lime, either monaxon or tetraxon; flagellated chambers large.

**Order 1. HOMOCCELA.** — Gastral layer continuous. Example: *Leucosolenia* (Fig. 77).

**Order 2. HETEROCCELA.** — Gastral layer discontinuous and restricted to flagellated chambers. Example: *Grantia* (Fig. 80).

**Class II. HEXACTINELLIDA.** — Deep-sea sponges; spicules triaxon, of silicon; canal system with thimble-shaped chambers. Example: *Euplectella aspergillum*, Venus' flower basket (Fig. 85).

**Class III. DEMOSPONGIA.** — Skeleton of siliceous spicules, not triaxon, or with spongin, or with both spicules and spongin; canal system derived from rhagon type (Fig. 92); most highly organized of phylum; majority of existing sponges.

**Order 1. TETRAXONIDA.** — Typically with tetraxon spicules. Example: *Thenea* (Fig. 87).

**Order 2. MONAXONIDA.** — With monaxon, but no tetraxon spicules. All fresh-water sponges belong to this order. Example: *Spongilla lacustris* (Fig. 90).

**Order 3. CERATOSA.** — Main skeleton of spongin. Example: *Euspongia officinalis*, the bath sponge (Fig. 91).

**Order 4. MYXOSPONGIA.** — Without skeleton; encrusting in habit. Example: *Oscarella* (Fig. 91).

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## CHAPTER III

### PHYLUM CŒLENTERATA

#### INTRODUCTION

The phylum CŒLENTERATA includes the polyps, jellyfishes, sea-anemones, and corals. All of these animals have a body wall consisting of two layers of cells, between which is a non-cellular substance, the mesoglea. Within the body is a single gastro-vascular cavity, or cœlenteron. Because of the presence of two cellular layers, all cœlenterates are said to be diploblastic. They are also acelomates, *i.e.* they do not possess a second body cavity, the cœlom. All cœlenterates are provided with nematocysts.

This phylum contains three classes, as follows:—

CLASS I. HYDROZOA. This class includes the fresh-water polyps, the small jellyfishes, the hydroid zoophytes, and a few stony corals.

CLASS II. SCYPHOZOA. Most of the large jellyfishes are placed in this class.

CLASS III. ANTHOZOA. In this class are included the sea-anemones, and most of the stony and horny corals.

In the following pages the fresh-water hydroid, *Hydra*, is described in detail because of its simplicity, abundance, and the ease with which it may be collected. *Obelia* represents a marine hydroid and *Gonionemus*, a hydroid jellyfish. The class SCYPHOZOA is introduced by the common large jellyfish, *Aurelia*, and the class ANTHOZOA by a sea-anemone, *Metridium*, and a coral, *As-trangia*.

#### 1. CLASS I. HYDROZOA

##### (1) HYDRA — A FRESH-WATER HYDROZOON

*Hydra* (Fig. 97) is a simple metazoon abundant in fresh-water ponds and streams. If a quantity of aquatic vegetation is gathered and placed in glass dishes full of water, these little fresh-water polyps may be found clinging to the plants and the sides and bottom of the dish. They are easily seen with the naked eye, being

from 2 to 20 mm. in length, and may be likened to a short thick thread frazzled at the unattached, distal end. The great variation in length is due to the fact that both body and tentacles are capable of remarkable expansion and contraction because of the presence of specialized muscle fibrils in many of the cells. A number of species of hydras are recognized by zoologists.

**External characters.**—The body of *Hydra* resembles an elastic tube which varies in length and thickness according as the animal is extended or contracted; in the former case it may reach a

length of 2 cm. At the distal end is a circlet of usu-

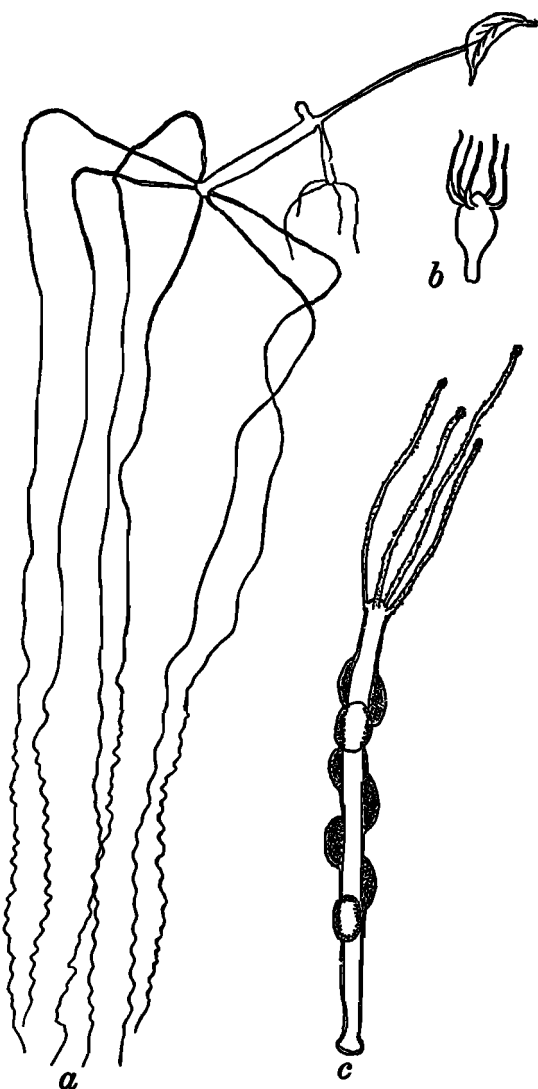


FIG. 97. — *Hydra oligactis*. a, Hanging from a leaf with tentacles well extended. Drawn from life. b, Position assumed when contracted. Drawn from life. c, Male bearing many testes. (After Hyman.)

ally from six to ten slender, finger-like projections called *tentacles*. The diameter of the body is frequently increased at

certain points by a distention due to the ingestion of large particles of food. Different species of *Hydra* differ in color but the color often depends on the character of the food and hence is not a constant feature. The part of the body which is usually attached to some object is known as the *foot* or *basal disk* and is referred to as the *proximal end*. The foot not only anchors the animal when at rest, but also serves as a locomotor organ. In the common brown species, *Hydra (fusca) oligactis*, the proximal region is a slender stalk and the distal region constitutes a sort of stomach. A conical elevation, the *hypostome*, occupies the distal end of the body. It is surrounded by the tentacles, and has at the top an opening, the *mouth*. This mouth is not the simple circular orifice often described, but is star-shaped, having clefts running out from the center toward each arm.

The *tentacles* are capable of remarkable expansion, and may stretch out from small blunt projections to very thin threads 7 cm. or more in length; in this condition they are so thin as to be barely visible even with a lens. They move independently capturing food and bringing it into the mouth. Their number varies considerably. Six hundred specimens of *Hydra viridissima* possessed from four to twelve tentacles each. These occurred in the following proportions: 54 per cent had eight; 24 per cent, seven; 15 per cent, nine; very few animals possessed a greater number than nine, and only occasionally was one found with less than seven. The number of tentacles increases with the size and age of the animal, although unfavorable conditions and extreme age result in a decrease.

Frequently specimens of *Hydra* are found which possess *buds* in various stages of development (Fig. 97, 98). Several buds are often found on a single animal, and these in turn may bear buds before detachment from the parent. In this way a sort of primitive *Hydra* colony is formed, resembling somewhat the asexual colonies of some of the more complex coelenterates to be described later. In *Hydra oligactis* there is a rather definite budding zone where stalk and body meet.

Reproductive organs may be observed on specimens of *Hydra* in the summer or autumn. Both an *ovary* and *testes* are produced on a single individual in most species; the former is knob-like, occupying a position about one third the length of the animal above the basal disk; the testes, usually two or more in number,

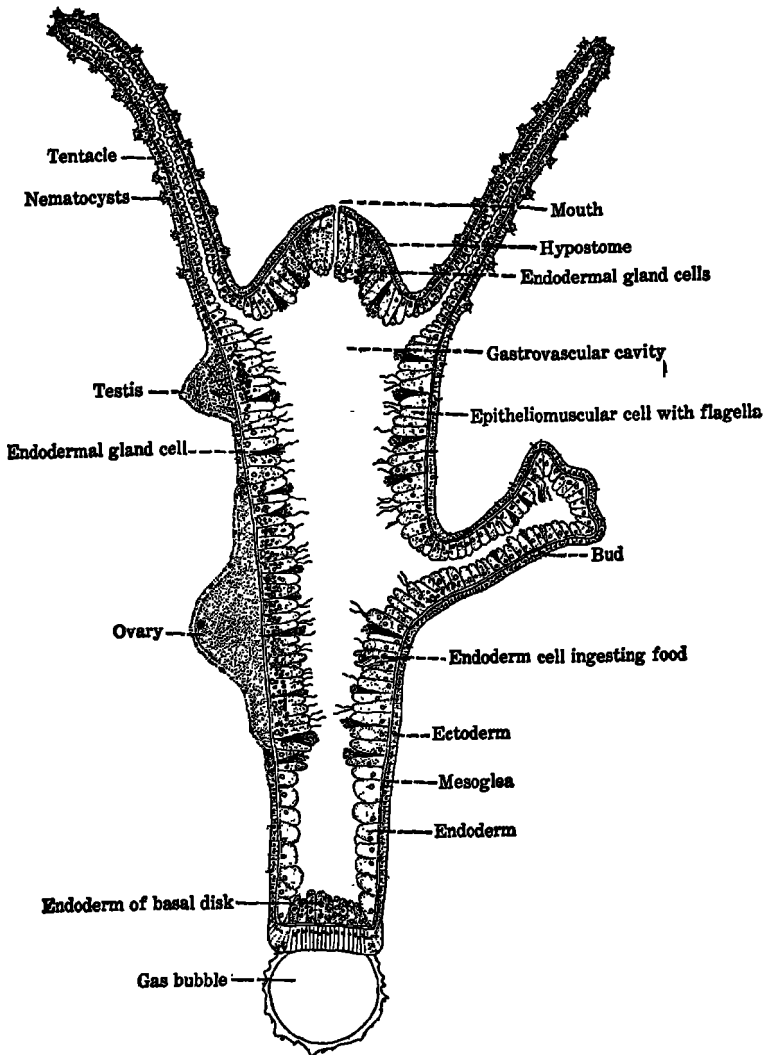


FIG. 98. — *Hydra*. Longitudinal section. (After Kepner and Miller.)



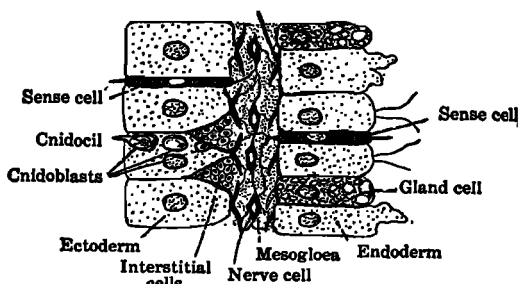


FIG. 99. — *Hydra*. Cross section of the body wall. (After Kükenthal modified.)

*ectoderm*, and an inner layer, the *endoderm*, twice as thick as the outer. Both layers are composed of *epithelial cells*. A thin space containing a jelly-like substance, the *mesogloea*, separates ectoderm

are conical elevations projecting from the distal third of the body (Figs. 97, 98).

**Morphology** (Fig. 98). — *Hydra* is a diploblastic animal consisting of two cellular layers, an outer thin layer, the

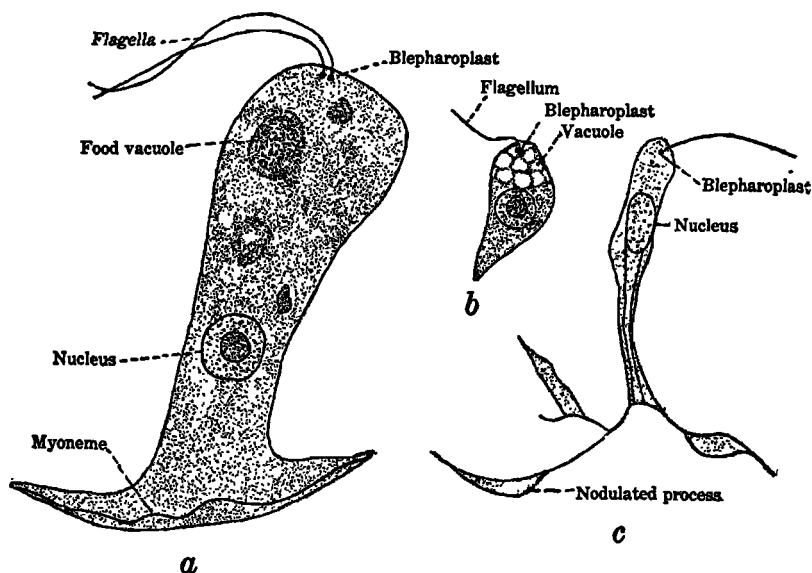


FIG. 100. — *Hydra oligactis*. Cellular elements enlarged. a, Epitheliomuscular cell. b, Secreting cell. c, Sensory cell. (After Burck.)

from endoderm. Not only the body wall, but also the tentacles, possess these three definite regions. The body, with the exception of the basal disk, is covered by a thin transparent *cuticle*. Both body and tentacles are hollow, the single central space being known as the *gastrovascular cavity* or *enteron*. At the bases of the tentacles

are sphincters that are capable of shutting off the connection between the cavity of the body and the cavities of the tentacles. Because of this, injurious material within the enteron may be prevented from reaching the tentacular cavities.

*Ectoderm* (Fig. 99). — The ectoderm is primarily *protective* and *sensory*, containing structures characteristic of these functions. Slight differences in structure are observable between the ectoderm of the tentacles and that of the body wall, while the latter differs from that of the basal disk. In the ectoderm of the body wall

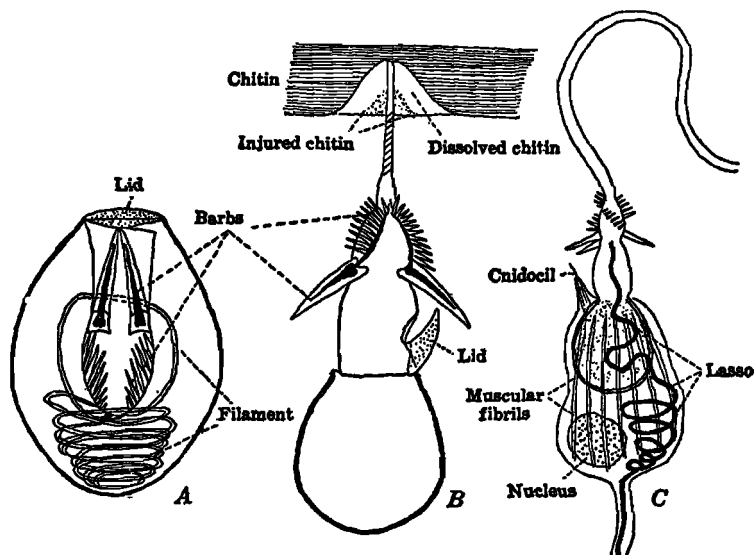


FIG. 101. — *Hydra*: nematocysts. A, Undischarged. B, Discharged. C, Discharged but retained within cnidoblast. (After Schulze.)

are two principal kinds of cells, large epitheliomuscular cells, and small interstitial cells. The latter give rise to cells called cnidoblasts which form nematocysts, and to both male and female germ cells. The *epitheliomuscular cells* (Fig. 100) are shaped like inverted cones. At their inner ends are one or more comparatively long (sometimes .38 mm.) unstriped *contractile fibers* which form a thin longitudinal muscular layer. These muscle fibers explain the remarkable powers of contraction exhibited by *Hydra* when stimulated. Near the middle of each cell, embedded in the alveolar cytoplasm, is a nucleus containing one or two nucleoli and a network of chromatin.

*Nematocysts* or stinging capsules are present on all parts of the body of *Hydra* except the basal disk, being most numerous on the tentacles (Fig. 98). Each is contained in a cell known as a *cnidoblast*. These in turn are embedded in little tubercles on the surface which give the animal a rough-appearing outline. The tubercles are ectoderm cells, each of which usually possesses one or more large nematocysts surrounded by a number of a smaller variety. Four kinds of nematocysts occur in *Hydra*. The largest is known as a *penetrant* and is .013 mm. long and .007 mm. thick; before being discharged it is pear-shaped and occupies almost the entire cell in which it lies (Fig. 101). Within it is a *coiled tube* at whose base are three large and a number of small *spines*. A second type is known as a *streptocline glutinant*; this type is large and cylindrical and pointed at the end where the thread is discharged. The thread, when discharged, bears a spiral row of minute barbs and tends to coil. *Stereocline glutinants* are smaller and oval with a thread that is straight and devoid of barbs when discharged. *Volvents* are small, pyriform nematocysts containing a thick, smooth thread in a single loop; the thread forms a tight coil when discharged. Projecting from the cnidoblast near the outer end of the nematocyst is a trigger-like spine, the *cnidocil*. Nematocysts may be exploded by adding a little acetic acid, or better, methyl green, to the water. The tube which is coiled within them is then everted. First, the base of the tube with the spines appears, and then the rest of the tube rapidly turns inside out. Nematocysts are able to penetrate the tissues of other animals, but only at their greatest speed and before eversion is completed. Even the extremely firm chitinous covering of insects may be punctured by these structures (Fig. 102, C). Touching the cnidocil was for a long time supposed to cause the explosion of the nematocysts, and for this reason it is known as a "trigger." One can easily prove, however, that mechanical shocks have no influence upon the nematocysts. Internal pressure produced either by distortion or by osmosis, is effective. For this reason chemicals which increase the osmotic pressure within the cnidoblast cause the eversion of the thread-like tube. In *Physalia* the nematocysts are exploded either by a combination of external and internal pressures, but in *Metridium* by internal pressure alone. "External pressure is produced by the contraction of a muscle-like envelope surrounding the nematocyst. Internal pressure is probably pro-

duced by a substance which is generated close to the nematocyst, penetrates its wall, and induces a swelling of its contents as acids swell gelatin." (Parker and Van Alstyne.) An animal when "shot" by nematocysts is immediately paralyzed, and sometimes killed, by a poison called hypnotoxin which is injected into it through the tube.

Nematocysts are developed from interstitial cells, each cell producing one nematocyst. "First a clear space appears in an in-

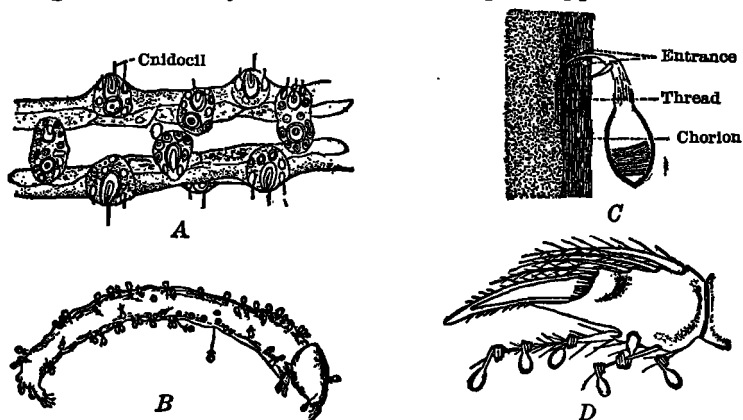


FIG. 102. — *Hydra*: nematocysts and their action. A, portion of a tentacle showing the batteries of nematocysts. B, insect larva covered with nematocysts as a result of capture by *Hydra*. C, a nematocyst piercing the chitinous covering of an insect. D, nematocysts holding a small animal by coiling about its spines. (A and B from Jennings; C and D from Toppe.)

terstitial cell; this space enlarges, it acquires a definite wall, and its contents stain deeply. Presently it elongates, and one end is produced to form the thread, which at its first appearance is everted and coiled round the outside of the sac. After a time the thread is introverted — it is not quite clear how — and the nematocyst assumes its final form. When nearly ripe a nematocyst, still contained in its mother cell or cnidoblast, migrates into the inside of an epitheliomuscular cell and approaches the surface. The external end of the cnidoblast is produced to form a cnidocil which perforates the cuticle. . . ." (Browne.) Since the tube of the nematocyst cannot be returned to the capsule, nor another one be developed by the cnidoblast, new capsules must be formed from interstitial cells to replace those already exploded.

The interstitial cells also develop at a certain period of the

year (September and October) into germ cells. The origin and history of these cells will be described later.

The *basal disk* differs somewhat in function from the rest of the body. It is the point by which *Hydra* attaches itself to solid objects, and for this purpose secretes a sticky substance. It is

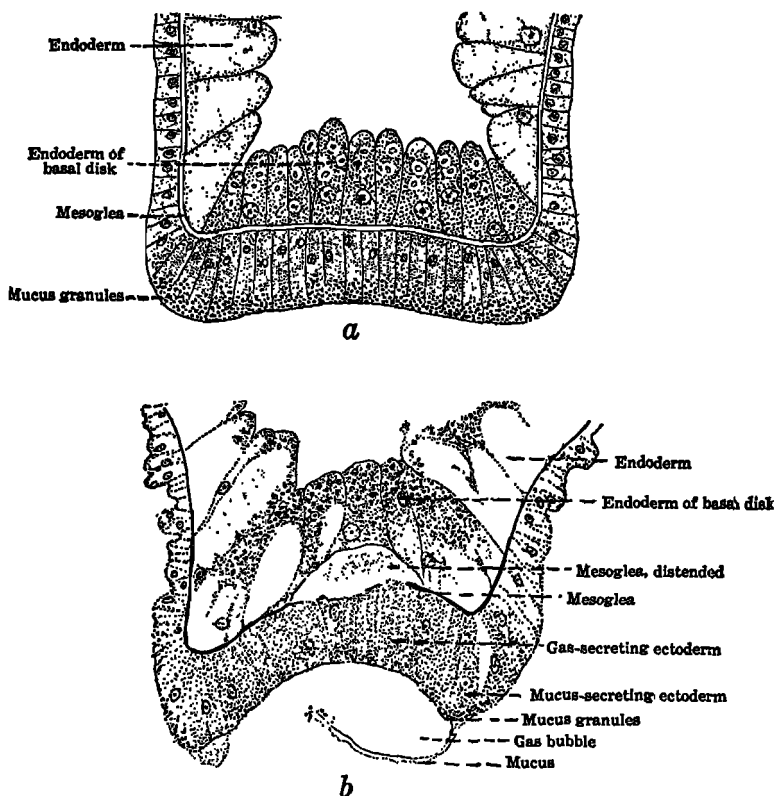


FIG. 103. — *Hydra oligactis*. a, Longitudinal section of basal region showing the endoderm cells of the basal disk containing food vacuoles and mucus-secreting cells of the ectoderm containing mucus granules with which the animal attaches itself to the substratum. b, Longitudinal section of basal region showing the formation of a gas bubble. (After Kepner and Thomas.)

also said to effect the movement of the animal from place to place by a sort of gliding motion, not yet fully explained, but possibly brought about by pseudopodia-like processes thrust out from some of the cells. Epitheliomuscular cells and a few interstitial cells are present, but no nematocysts are to be found here. The columnar

epitheliomuscular cells are not only provided with contractile fibers at their bases, but, being secretory, also contain a large number of small refringent granules, as shown in figure 103, *a*. Certain ectoderm cells of the basal disk secrete a gas which may be confined within the mucus thus forming a bubble (Figs. 98, 103, *b*). Such a gas bubble may lift the *Hydra* to the surface where it breaks and spreads out like a raft from which the animal hangs suspended in the water.

The *tentacles* (Fig. 98) are provided with an ectoderm consisting of large flat cells, thin at the edges and thick in the center. The thicker portions give the surface of the tentacle a lumpy appearance. In the center of each thickening is a nucleus around which are embedded sometimes as many as twelve nematocysts each in its own cnidoblast (Fig. 102, *A*). The cnidocils projecting from the cnidoblasts resemble groups of cilia. Each cnidoblast is drawn out at its base into a contractile fibril which enters the longitudinal muscular sheet at the base of the ectoderm cells.

*Endoderm* (Fig. 98). — The inner layer of cells, the endoderm, occupies about two thirds of the body wall. Its functions are *digestive* and *secretory*. The digestive cells are long and club-shaped, with transverse muscular fibrils at their base, forming a circular sheet of contractile substance. Many of them are provided with from one to five flagella which are non-tapering, lash-like processes that arise from a cytoplasmic granule or blepharoplast (Fig. 100). The epitheliomuscular cells possess one or more flagella; the secreting cells, one or two; and the sensory cells, one. Besides flagella *pseudopodia* may also be thrust out from the free end (Fig. 99). The flagella create currents in the gastrovascular fluid, and the pseudopodia capture solid food particles. The endoderm of the hypostome contains secreting cells that appear to produce a secretion of importance during the ingestion of food. The internal structure of these cells differs before and after the animal is fed. In a starving *Hydra* large vacuoles appear, almost completely filling the cell, the protoplasm being reduced to a thin layer near the cell wall; after a meal, however, the cells are gorged with nutritive spheres, many of which, especially the oil globules, migrate into the ectoderm and are stored near the periphery.

The *glandular cells* are smaller than the digestive cells, and lack the contractile fibrils at their base (Fig. 99). They also differ in appearance according to their metabolic activity: some are

filled with large vacuoles containing secretory matter, while others, having discharged their secretum, appear crowded with fine granules. Interstitial cells are found lying at the base of the other endoderm cells.

The tentacles contain endoderm cells apparently devoid of muscular fibers. Gland cells are also absent from this region. The endoderm of the basal disk is provided with only a few glandular cells.

*Mesoglea* (Figs. 98, 99). — The mesoglea in *Hydra* is so thin as to be difficult to find, even when highly magnified; in some of the other Coelenterates this layer is very thick, constituting by far the largest part of the body.

*Nervous system.* — *Hydra* possesses a nervous system, but complicated staining methods are necessary to make it visible. In

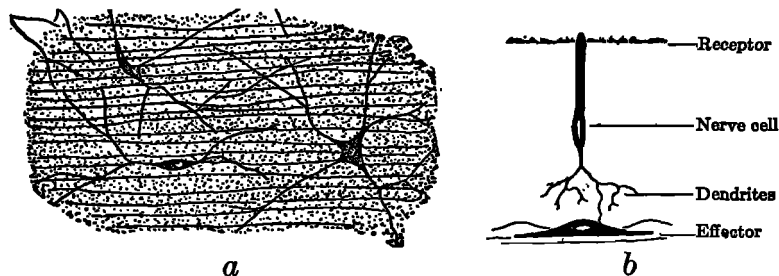


FIG. 104. — Nerve cells of *Hydra*. a, Plexus of nerve cells in the ectoderm; the parallel lines represent longitudinal muscle fibers. b, Receptor-effector system of a hydrozoan. (a, after Schneider; b, after Parker.)

the ectoderm there is a sort of plexus of nerve cells connected by nerve fibers (Figs. 100, 104, a). Sensory cells in the surface layer of cells (Fig. 99) serve as external organs of stimulation, and are in direct continuity with fibers from the nerve cells. Some of the nerve cells send processes to the muscle fibers of the epitheliomuscular cells, and are therefore motor in function (Fig. 104, b). No processes from the nerve cells to the nematocysts have yet been discovered, though they probably occur. The endoderm of the body also contains nerve cells, but not so many as are present in the ectoderm (Fig. 99).

*Nutrition.* — *Food.* — The food of *Hydra* consists principally of small animals that live in the water. Of these may be mentioned small crustaceans such as *Cyclops*, annelids, and insect larvæ. *Hydra* normally rests with its basal disk attached to some object and its body and tentacles extended out into the water. In this

position it occupies a considerable amount of hunting territory. Any small aquatic animal swimming in touch with a tentacle is at once shot full of nematocysts (Fig. 102, *B*), which not only seem to paralyze it, but also to hold it firmly. There is some evidence to prove that the tentacles are able to secrete a fluid which serves to paralyze the animal without the aid of nematocysts. The viscid surface of the tentacle aids in making sure that the victim does not escape.

*Ingestion.* — Ingestion takes place as follows: First, the tentacle, which has captured the prey, bends toward the mouth with its load of food. The other tentacles not only assist in this, but may use their nematocysts in quieting the victim. The mouth often begins to open before the food has reached it. The edges of the mouth gradually enclose the organism and force it into the gastrovascular cavity. The body wall contracts behind the food and forces it down. Frequently organisms many times the size of the *Hydra* are successfully ingested.

*Reactions to food.* — It is not uncommon to find hydras that will not react to food when it is presented to them. This is due to the fact that these animals will eat only when a certain interval of time has elapsed since their last meal. The physiological condition of *Hydra*, therefore, determines its response to the food stimulus. The collision of an aquatic organism with the tentacle of *Hydra* is not sufficient to cause the food-taking reaction, since it has been found that not only a mechanical stimulus, but also a chemical stimulus must be present. A very hungry *Hydra* will even go through the characteristic movements when it is excited by the chemical stimulus alone. This has been shown by the following experiment. When the tentacles and hypostome of a moderately hungry *Hydra* are brought into contact with a piece of filter paper, which has been soaked for a time in the same culture medium, there is no response. If the filter paper is then soaked in beef juice and offered to the *Hydra*, the usual food reactions are given.

Beef juice alone calls forth no response in a moderately hungry animal; but does inaugurate the normal reflex, if a very hungry specimen is selected for the experiment. The conclusion reached is that well-fed hydras will not respond to either mechanical or chemical stimuli when acting alone or in combination; that moderately hungry animals will react to a combination of the two, and



that hungry animals will exhibit food-taking movements even if a chemical stimulus alone is employed.

**Digestion.**—Immediately after the ingestion of food the gland cells in the endoderm show signs of great activity; their nuclei enlarge and become granular. This is due probably to the formation of enzymes which are discharged into the gastrovascular cavity and begin at once the dissolution of the food. The action of the digestive juices is made more effective by the churning of the food as the animal expands and contracts. The cilia extending out into the central cavity also aid in the dissolution of the food by creating currents. This method of digestion differs from that of *Amœba* and *Paramœcium* in being carried on outside of the cell; i.e. extracellular. Intracellular digestion also takes place in *Hydra*; the pseudopodia thrust out by the endoderm cells seize and engulf particles of food which are dissolved within the cells. However, most of the food is digested in the gastrovascular cavity. The digested food is absorbed by the endoderm cells; part of it, especially the oil globules, is passed over to the ectoderm, where it is stored.

**Egestion.**—All insoluble material is egested from the mouth. This is accomplished by “a very sudden squirt” which throws the débris to some distance.

**Symbiosis.**—One species of *Hydra*, *H. viridissima*, is green in color because of the presence within the endoderm cells of a unicellular alga, *Chlorella vulgaris*. As in *Paramœcium bursaria*, the plant uses some of the waste products of metabolism of the *Hydra*, and the *Hydra* uses some of the oxygen resulting from the process of photosynthesis in the plant. This condition is one of symbiosis.

**Behavior.**—*Hydra viridissima* gives a more prompt and decisive response when stimulated than any other species of *Hydra*, and for this reason its behavior has been studied more thoroughly than that of the others. The following paragraphs have been compiled largely from experiments upon green hydras, although enough work has been done with other forms to prove that their reactions are practically the same, only more sluggish.

**Normal position of *Hydra*** (Fig. 97).—Hydras may be found attached to the sides or bottom of an aquarium, to parts of water plants, or hanging from the surface film. Usually they are near the top where more oxygen can be obtained from the water than at

greater depths. If attached to the bottom, the body is usually held upright; if to the sides, the body is in most cases horizontal, the hypostome generally being lower than the foot; and if to the surface film, the body is allowed to hang directly downward. Suspension from the surface film may be compared with that of a needle placed on the surface of the water. Threads of a gelatinous substance, extending out from the basal disk, help sustain the body, while in some cases a gas bubble attached to the foot keeps the animal afloat. The position of rest in every case gives the *Hydra*

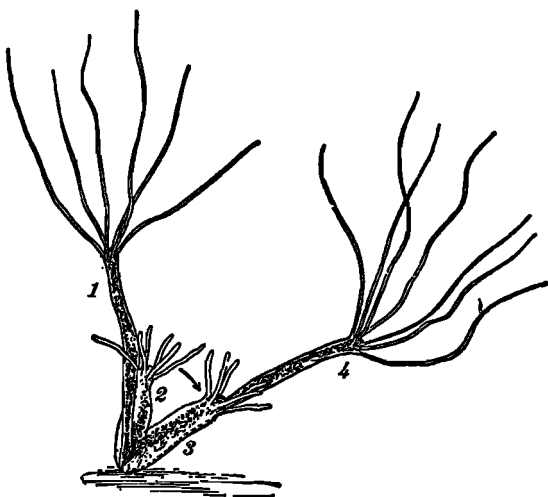


FIG. 105. — Spontaneous changes of position in an undisturbed *Hydra*. Side view. The extended animal (1), contracts (2), bends to a new position (3), and then extends (4). (From Jennings.)

the greatest opportunities for capturing food, since in this condition it has control of a large amount of territory.

*Spontaneous movements.* — All the movements of *Hydra* are the result of the expansion or contraction of the muscle fibers, and are produced by two kinds of stimuli, internal, or spontaneous, and external. Spontaneous movements may be observed when the animal is attached and undisturbed. At intervals of several minutes the body, or tentacles, or both, contract suddenly and rapidly, and then slowly expand in a new direction. Hungry specimens are more active than well-fed individuals. The result is to bring the animal into a new part of its surroundings, where more food may be present (Fig. 105). These movements finally cease, and the animal's position is changed by locomotion.

*Locomotion.* — Movement from place to place is effected in several ways. In most cases the animal bends over (Fig. 106, 1) and attaches itself to the substratum by its tentacles (2), probably

with the aid of pseudopodia thrust out by the ectoderm cells. The basal disk is then released and the animal contracts (3). It then expands (4), bends over in some other direction and attaches its foot (5). The tentacles now loosen their hold and an upright position is regained (6). The whole process has been likened to the looping locomotion of a measuring worm. At other times the animal moves from place to place while inverted by using its tentacles as legs. Locomotion may also result from the gliding of the foot along the substratum, and considerable distances are

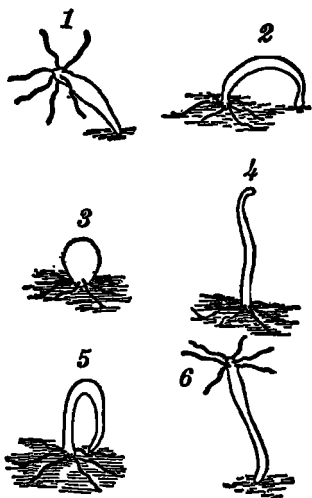


FIG. 106. — Locomotion in *Hydra*: moving like a measuring worm. (After Wagner.)

sometimes covered in this way. In *Hydra oligactis* the tentacles may be attached to some object, the basal disk freed, and the body drawn up to the object by the contraction of the tentacles.

#### Reactions to external stimuli.—

**Contact.**—*Hydra* reacts to various kinds of special stimuli. Reaction to contact accounts for its temporary fixed condition. The attachment while in the resting attitude is a result of this reaction, and not a response to gravity, since hydras have the longitudinal axis of the body directed at every possible angle regardless of the force of gravity. Mechanical shocks, such as the jarring of the watch glass containing a

specimen, or the agitation of the surface of the water, cause a rapid contraction of a part or all of the animal. This is followed by a gradual expansion until the original condition is regained.

Mechanical stimuli may be *localized* or *non-localized*. That just noted is of the latter type. *Local stimulation* may be accomplished by touching the body or tentacles with the end of a fine glass rod. It has been noted that the stimulation of one tentacle may cause the contraction of all the tentacles, or even the contraction of both tentacles and body. This shows that there must be some sort of transmission of stimuli from one tentacle to another and to the body. The structure of the nervous system would make this possible.

*Light.* — There is no definite response to light, although the final result is quite decisive. If a dish containing hydras is placed so that the illumination is unequal on different sides, the animals will collect in the brightest region, unless the light is too strong, in which case they will congregate in a place where the light is less intense. *Hydra* therefore has an optimum with regard to light. The movement into or out of a certain area is accomplished by a method of "trial and error." When put in a dark place *Hydra* becomes restless and moves about in no definite direction; but if white light is encountered, its locomotion becomes less rapid and finally ceases altogether. The value to the organism of such a reaction is considerable, since the small animals that serve as food for it are attracted to well-lighted areas. *Colored lights* have the same effect as darkness; blue, however, is preferred by *Hydra* to white.

*Temperature.* — The reactions of *Hydra* to changes in temperature are also indefinite, although in many cases they enable the animal to escape from a heated region. No locomotory change is produced by temperatures below 31° C.; at this temperature, however, the basal disk is released and the animal takes up a new position either away from the heated area or further into it. In the former case the *Hydra* escapes, in the latter it may escape if subsequent movements take it away from the injurious heat, otherwise it perishes. *Hydra* does not move from place to place if the temperature is lowered; it contracts less rapidly, and finally ceases all its movements when the freezing point is approached.

*Electric current.* — An attached *Hydra*, when subjected to a weak constant electric current, bends toward the anode, its body finally becoming oriented with the basal disk toward the cathode and the anterior end toward the anode side. The entire animal then contracts. In an animal attached by the tentacles a similar bending occurs, but the basal disk in this case is directed toward the anode. These reactions are caused by local contractions on the anode side for which the electric current is directly responsible.

*Hydra* shows no reactions to currents of water. When placed in a current of water it neither orients itself in a definite way nor moves either up or down stream. - -

*General remarks.* — It is evident from the above outline of the reactions of *Hydra* to stimuli that the only movements

involved are produced by contraction and expansion of the body when attached, and by undirected changes of position. Being radially symmetrical, the body may be flexed in any direction.

*Local stimuli*, such as the application of heat or a chemical to a limited area of the body, causes a contraction of the part affected and a bending in that direction. This results in the movement of the tentacular region toward the stimuli, and the contraction of the entire animal follows, thus carrying it out of the influence of the stimulus.

*Non-localized stimuli*, such as the jarring of the vessel containing the animals, produces, immediately, a contraction of the entire body, which, in most cases, is beneficial, since it removes it from an injurious agent. If, however, this simple contraction is not effective, as in the case of a constant application of heat, the *Hydra* usually resorts to some other reaction, *e.g.* locomotion, which often enables it to escape from the injurious stimulus.

Finally, it should be remembered that the physiological condition of the animal determines to a large extent the kind of reactions produced, not only spontaneously, but also by external stimuli. "It decides whether *Hydra* shall creep upward to the surface and toward the light, or shall sink to the bottom; how it shall react to chemicals and to solid objects; whether it shall remain quiet in a certain position, or shall reverse this position and undertake a laborious tour of exploration." (Jennings.)

**Reproduction.** — Reproduction takes place in *Hydra* both *asexually* and *sexually*; in the former case by budding, in the latter, by the production of a fertilized egg. Longitudinal and transverse division have been described in *Hydra*, but apparently are not methods of reproduction; they are simply processes that enable an abnormal animal to regain its normal shape.

**Budding** (Figs. 97, 98). — Asexual reproduction by budding is easily observed in the laboratory. Superficially the bud appears first as a slight bulge in the body wall. This pushes out rapidly into a stalk which soon develops a circlet of blunt tentacles about its distal end. The cavities of both stalk and tentacles are at all times directly connected with that of the parent. When full grown, the bud becomes detached and leads a separate existence. The details of the process are briefly as follows. The interstitial cells in a certain region increase in number and volume, producing a slight outbulging of the ectoderm. The growing region is located at

the point where the edges of the protrusion meet the body wall. Here the cells are well fed and multiply actively. The ectoderm and endoderm cells of the parent give rise to the corresponding cells of the bud. When the bud is fully grown, the ectoderm cells at its proximal end secrete a sticky substance which is used later for its attachment. The endoderm cells in the same region then unite, separating the cavity of the bud from that of the parent. Finally, the bud becomes detached. The food supply determines the rate of growth of the bud, and a bud may be entirely absorbed by a starving animal.

The tentacles of the bud arise first as two outgrowths opposite each other. The third tentacle develops between these on the side toward the oral end of the parent; the fourth, opposite the third and the fifth and sixth on either side of the third.

**Sexual reproduction.** — Whether or not there are definite germ cells in the adult *Hydra* is still open to question. So far as is known, both ova and spermatozoa arise from indifferent interstitial cells. Hydras are, with the exception of *H. oligactis*, hermaphroditic; the latter are either male or female. In *H. oligactis* the sex organs are located on the body and not on the stalk. There may be as many as 20 or 30 testes, low and rounded in shape and devoid of nipples. The sexual state can be induced in this species by lowering the temperature; which accounts for the appearance of sex organs in the autumn. During asexual reproduction, sex is inherited, since buds produce the same kind of sex organs as the parent, and all members of a clone are of the same sex.

**Spermatogenesis.** — The male cells of *Hydra* are formed in little conical elevations called *testes* which project from the surface of

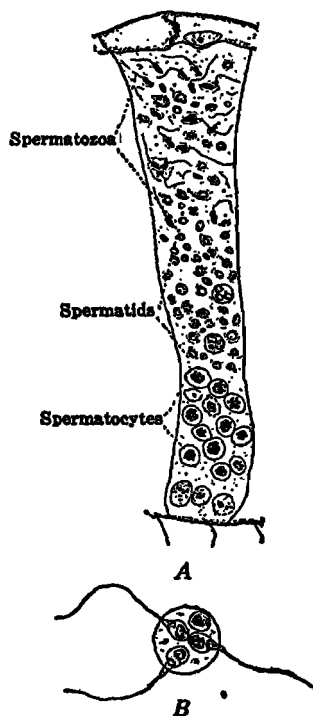


FIG. 107. — Parts of the testis of *Hydra*. A, A single cyst. B, Developing spermatozoa. (From Tannreuther.)

the body (Figs. 97, c, 98). The testis arises within the ectoderm from interstitial cells. A single interstitial cell divides mitotically; then adjacent interstitial cells also divide, multiplication continuing until the ectoderm becomes distended. An indefinite number of long multinucleated cysts (Fig. 107, A) are formed within the testis, each cyst being the product of a single or several interstitial cells. Each interstitial cell is a primordial germ cell; it gives rise by mitosis to a variable number of spermatogonia, which contain twelve chromosomes, the somatic number. Reduction in the number of chromosomes to six occurs just after the spermatogonia have divided to form the primary spermatocytes. The latter give rise to secondary spermatocytes which divide at once, producing spermatids. These two spermatocyte divisions take place without the formation of cell walls, *i.e.* each primary

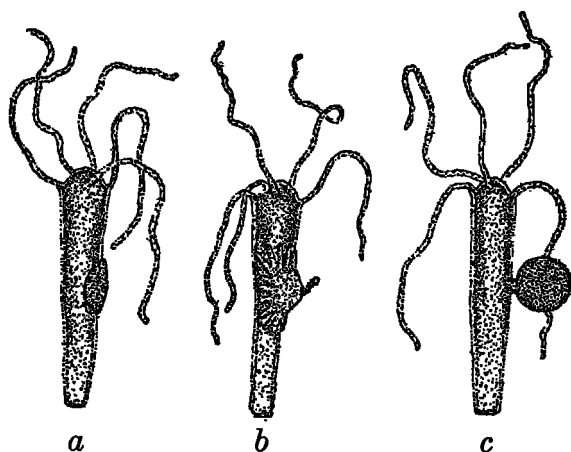


FIG. 108. — *Hydra viridissima*. Stages in the growth of the egg. a, Young oogonium. A cross section through this oogonium is shown in Fig. 109. b, Oocyte with many pseudopodia. c, Primary oocyte with complete amount of yolk. (After Kepner and Looper.)

spermatocyte develops into a four-nucleated cell which represents the four spermatids. Within this cell the spermatids transform into spermatozoa (Fig. 107, B). A single cyst may contain representatives of all of these cell generations — spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids, and spermatozoa. The mature spermatozoa break out of the vesicle in which they are formed, and swim about in the distal end of the cyst

(Fig. 107, A); they finally reach the outside by way of a minute temporary opening in the end of the cyst. The mature spermatozoa swim about in the water searching for an egg; their activity continues from one to three days.

*Oogenesis.* — The egg is first distinguished from the interstitial cells of the ectoderm by its slightly greater size, its spherical shape, and the comparatively large volume of its nucleus. As the eggs grow in size the neighboring interstitial cells increase in number by mitosis, and also become larger. The whole structure may at this time be called an ovary (Figs. 98, 108, 109). The nourishment of the egg is at first similar to that of the other ectoderm cells, but later disintegration and resorption of adjacent interstitial cells takes place. Yolk is elaborated from material that enters from the endoderm. Usually only one egg is developed in a single ovary (Fig. 109), but sometimes two may arise and complete their development side by side. In most cases, however, when two or more eggs are contained in one ovary, their adjacent walls dissolve and one of the nuclei survives while the others disintegrate. As the ovum grows it becomes amoeboid in shape, showing distinct pseudopodia (Fig. 108, b); these are drawn in when it has reached its full size. The egg is now nearly spherical (Fig. 108, c), and is surrounded by a single layer of ectoderm cells. Maturation then takes place. Two polar bodies are formed, the first being larger than the second. During maturation the number of chromosomes is reduced from the somatic number, twelve, to six. This occurs at the end of the growth period. Now an

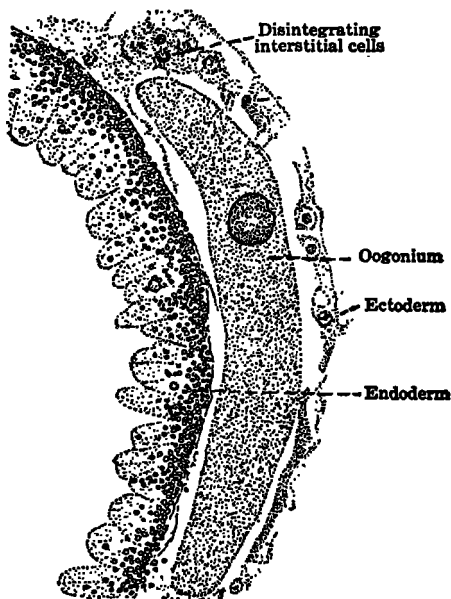


FIG. 109. — *Hydra viridissima*. Cross section through oogonium shown in Fig. 108, a. (After Kepner and Looper.)



opening appears in the ectoderm and the egg is forced out, finally becoming free on all sides except where attached to the animal.

**Fertilization.** — Fertilization usually occurs within two hours. Several sperms penetrate the egg membrane, but only one enters the egg itself. If not fertilized within twenty-four hours, the egg becomes sterile. The sperm brings a nucleus containing six chromosomes into the egg. The male and female nuclei unite, forming the fusion nucleus.

**Embryology.** — *Cleavage*, which now begins, is total and regular. A well-defined cleavage cavity is present at the end of the third cleavage, *i.e.* the eight-celled stage. When the *blastula* is completed, it resembles a hollow sphere with a single layer of epithelial cells composing its wall. These cells may be called the primitive ectoderm. By mitotic division they form endoderm cells which drop into the cleavage cavity, completely filling it. The *gastrula*, therefore, is a solid sphere of cells differentiated into a single outer layer, the ectoderm, and an irregular central mass, the endoderm. The ectoderm surrounds the gastrula with two envelopes. The outer is a thick chitinous shell covered with sharp projections; the inner is a thin gelatinous membrane.

**Hatching.** — The embryo in this condition separates from the parent and falls to the bottom, where it remains unchanged for several weeks. Then interstitial cells make their appearance. A subsequent resting period is followed by the breaking away of the outer chitinous envelope and the elongation of the escaped embryo. Mesoglea is now secreted by the ectoderm and endoderm cells; a circlet of tentacles arises at one end and a mouth appears in their midst. The young *Hydra* thus formed soon grows into the adult condition.

**Depression.** — Hydras, both in nature and in laboratory cultures, appear to undergo stages of depression during which the tentacles shorten and gradually disappear and the body of the animal becomes shorter due to the disintegration of the tissues at the distal end. Finally only a ball-like mass of cells representing the basal end remains, and this soon disintegrates. Depression appears to be due to a lowered metabolic state which may be produced by rich feeding, high temperature, senescence, fouling of the culture water, lack of oxygen, or transfer to clean fresh water. Recovery from depression may occur spontaneously or may be induced by transferring the animals to a culture in which other

hydras are flourishing. Often within an hour the body begins to elongate and tentacles to appear.

**Regeneration.** — An account of the phenomenon of regeneration is appropriate at this place, since the power of animals to restore lost parts was first discovered in *Hydra* by Trembley in 1740. This investigator found that if hydras were cut into two, three, or four pieces, each part would grow into an entire animal (Fig. 110, c).

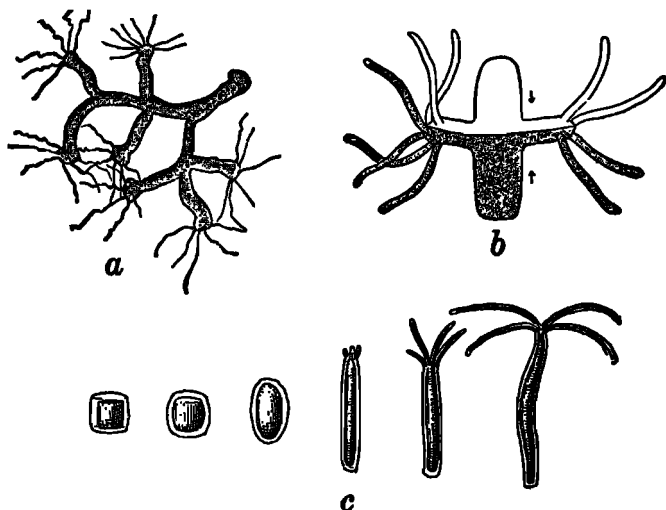


FIG. 110. — *Hydra*. Regeneration and grafting. a, A seven-headed *Hydra* resulting from regeneration after the distal ends were split lengthwise. b, Parts of two hydras grafted together. c, The regeneration of an entire *Hydra* from a small piece of the stalk. (After several authors.)

Other experimental results obtained by Trembley are that the hypostome together with the tentacles, if cut off, produce a new individual; that each piece of a *Hydra* split longitudinally into two or four parts, becomes a perfect polyp, that when the head end is split in two and the parts separated slightly a two-headed animal results (Fig. 110, a); and that a specimen when turned inside out is able to readjust itself to new conditions forced upon it.

**Regeneration** may be defined as the replacing of an entire organism by a part of the same. It takes place not only in *Hydra*, but in many other coelenterates, and in some of the representatives of almost every phylum of the animal kingdom. *Hydra*, however, is the species that has been most widely used for experimentation. Pieces of *Hydra* that measure  $\frac{1}{8}$  mm. or more in diameter are

capable of becoming entire animals (Fig. 110, *c*). The tissues in some cases restore the lost parts by a multiplication of their cells; in other cases, they are worked over directly into a new but smaller individual.

Recent experiments have shown that when pieces of hydras too small to regenerate are allowed to come into contact with one another they fuse. The endoderm appears to initiate this fusion and controls the process. The endoderm of one piece may fuse with the endoderm of an adjoining piece rapidly. Ectoderm does not fuse with ectoderm nor with endoderm, and mesoglea appears to have little or no power of fusion. Fusion, as indicated by tissue culture experiments, appears to be the result of the interlacing of amoeboid processes sent out by the endoderm cells of the pieces in contact. As a result of this fusion a plate-like body is formed which may, within a period of about twelve hours, develop into a sac. This sac becomes attached at a certain point which is the basal disk; it then elongates; tentacles bud out at the distal end and a normal hydra results. (Papenfuss.)

*Grafting.* — Parts of one *Hydra* may easily be grafted upon another (Fig. 110, *b*). In this way many bizarre effects have been produced. Parts of two hydras of two species have also been successfully united.

Space will not permit a detailed account of the many interesting questions involved in the phenomena of regeneration, but enough has been given to indicate the nature of the process. The benefit to the animal of the ability to regenerate lost parts is obvious. Such an animal, in many cases, will succeed in the struggle for existence under adverse conditions. Regeneration takes place continually in all animals; for example, new cells are produced in the epidermis of man to take the place of those that are no longer able to perform their proper functions. Both internal and external factors have an influence upon the rate of regeneration and upon the character of the new part. Temperature, food, light, gravity, and contact are some of the external factors. In man, various tissues are capable of regeneration; for example, the skin, muscles, nerves, blood vessels, and bones. Lost parts are not restored in man, because the growing tissues do not co-ordinate properly. Many theories have been advanced to explain regenerative processes, but none has gained sufficient acceptance to warrant its inclusion here.

(2) OBELIA — A COLONIAL HYDROZOON

*Obelia* (Fig. 111) is a colonial coelenterate which lives in the sea, where it is usually attached to rocks, to wharves, or to *Laminaria*, *Rhodymenia*, and other algæ. It may be found in low water and to a depth of forty fathoms along the coast of northern Europe and from Long Island Sound to Labrador.

**Anatomy and physiology.** — An *Obelia* colony consists of a basal stem, the *hydrorhiza*, which is attached to the substratum; this gives off at intervals upright branches, known as *hydrocauli*. At every bend in the zigzag hydrocaulus a side branch arises. The stem of this side branch is ringed and is expanded at the end into a hydra-like structure, the *hydranth*. A single polyp consists of a hydranth and the part of the stalk between the hydranth and the point

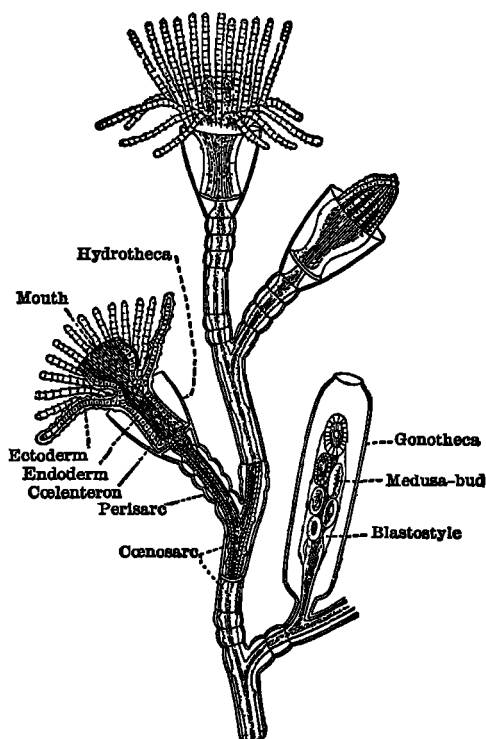


FIG. 111. — *Obelia*. Part of a colony.  
(After Parker and Haswell.)

of origin of the preceding branch. Full-grown colonies usually bear reproductive members (*gonangia*) in the angles where the hydranths arise from the hydrocaulus.

The *Obelia* colony, as just described and as illustrated in figure 111, resembles the structure that would be built up by a budding *Hydra* if the buds were to remain attached to the parent and in turn produce fixed buds.

All of the soft parts of the *Obelia* colony are protected by a chitinous covering called the *perisarc*; this is ringed at various

places and is expanded into cup-shaped *hydrothecæ* to accommodate the hydranths, and into *gonothecæ* to enclose the reproductive members. A shelf which extends across the base of the hydrotheca serves to support the hydranth. The soft parts of the hydrocaulus and of the stalks of the hydranths constitute the *cœnosarc*, and are attached to the perisarc by minute projections. The cœnosarcular cavities of the hydrocaulus open into those of the branches and thence into the hydranths, producing in this way a common *gastrovascular cavity*.

A longitudinal section of a hydranth and its stalk (Fig. 111) shows the cœnosarc to consist of two layers of cells — an outer

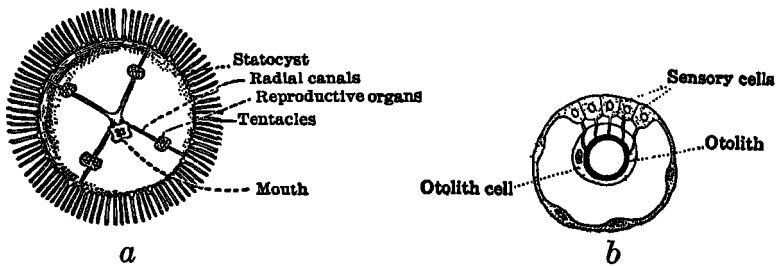


FIG. 112. — *Obelia*. a, Medusa. b, Statocyst. (a, after Parker and Haswell; b, after Kerr.)

layer, the *ectoderm*, and an inner layer, the *endoderm*. These layers are continued into the hydranth. The *mouth* is situated in the center of the large knob-like *hypostome*, and the *tentacles*, about thirty in number, are arranged around the base of the hypostome in a single circle. Each tentacle is solid, consisting of an outer layer of ectoderm cells and a single axial row of endoderm cells; at the extremity are a large number of nematocysts. The hydranth captures, ingests, and digests food as in *Hydra*.

The *reproductive members* arise, as do the hydranths, as buds from the hydrocaulus, and represent modified hydranths. The central axis of each is called a *blastostyle*, and together with the gonothecal covering is known as the *gonangium*. The blastostyle gives rise to *medusa-buds* which soon become detached and pass out of the gonotheca through the opening in the distal end.

Some of the *medusæ* of *Obelia* (Fig. 112, a) produce eggs, and others produce spermatozoa. The fertilized eggs develop into colonies like that which gave rise to the medusæ. The medusæ provide for the dispersal of the species, since they swim about

in the water and establish colonies in new habitats. The medusa of *Obelia* is shaped like an umbrella with a fringe of tentacles and a number of organs of equilibrium on the edge (Fig. 112, b). Hanging down from the center is the *manubrium* with the mouth at the end. The gastrovascular cavity extends out from the cavity of the manubrium into four *radial canals* on which are situated the reproductive organs.

The *germ cells* of the medusæ of *Obelia* arise in the ectoderm of the manubrium, and then migrate along the radial canals to the reproductive organs. When mature, they break out into the water. The eggs are *fertilized* by spermatozoa which have escaped from other medusæ. *Cleavage* is similar to that of *Hydra*, and a hollow *blastula* and solid *gastrula-like* structure are formed. The gastrula-like structure soon becomes ciliated and elongates into a free-swimming larva called a *planula*. This soon acquires a central cavity, becomes fixed to some object, and proceeds to found a new colony. The physiological processes of *Obelia* are similar to those described in *Hydra*.

### (3) GONIONEMUS — A HYDROZOAN MEDUSA

The structure of a hydrozoan jellyfish or medusa may be illustrated by *Gonionemus* (Fig. 113). This jellyfish is common along the eastern coast of the United States. It measures about half an inch in diameter, without including the fringe of tentacles around the margin. In general form it is similar to the medusa of *Obelia* (Fig. 112, a). The convex or aboral surface is called the *exumbrella*; the concave, or oral surface, the *subumbrella*.

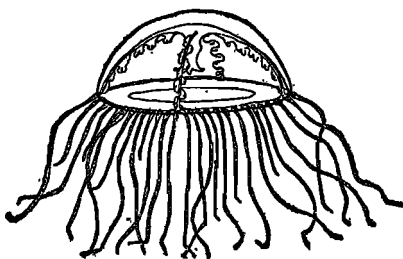


FIG. 113. — *Gonionemus*: a hydrozoan jellyfish. (After Hargitt, from Washburn.)

The subumbrella is partly closed by a perforated membrane called the *velum*. Water is taken into the subumbrellar cavity and is then forced out through the central opening in the velum by the contraction of the body; this propels the animal in the opposite direction, thus enabling it to swim about.

The *tentacles*, which vary in number from sixteen to more than eighty, are capable of considerable contraction. Near their tips

are *adhesive* or *suctorial pads* at a point where the tentacle bends at a sharp angle. Hanging down into the subumbrellar cavity is the *manubrium* with the *mouth* at the end surrounded by four frilled *oral lobes*. The mouth opens into a *gastrovascular cavity* which consists of a central "*stomach*" and four *radial canals*. The radial canals enter a *circumferential canal* which lies near the margin of the umbrella.

The cellular layers in *Gonionemus* are similar to those in *Hydra*, but the *mesoglea* is extremely thick and gives the animal a jelly-like consistency. Scattered about beneath the ectoderm are many *nerve cells*, and about the velum is a *nerve ring*. *Sensory cells* with a tactile function are abundant on the tentacles. The margin of the umbrella is supplied with two kinds of sense organs: (1) at the base of the tentacles are round bodies which contain pigmented endoderm cells and communicate with the circumferential canal; (2) between the bases of the tentacles are small outgrowths which are probably organs of equilibrium and, therefore, *statocysts*.

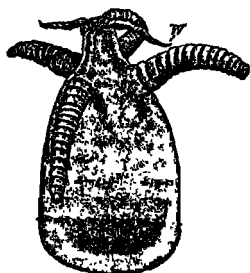


FIG. 114. — *Gonionemus*: hydra-like stage in development. One of the tentacles is carrying a worm (*W*) to the mouth. The tentacles are in a contracted state. (After Perkins.)

*Muscle fibers*, both exumbrella and subumbrella, are present, giving the animal the power of *locomotion*.

Suspended beneath the radial canals are the sinuously folded *reproductive organs* or *gonads*. *Gonionemus* is dioecious, one individual producing either eggs or spermatozoa. These reproductive cells break out directly into the water, where *fertilization* takes place. A ciliated *planula* develops from the egg as in *Obelia*. This soon becomes fixed to some object, and a mouth appears at the unattached end. Then four tentacles grow out around the mouth and the hydra-like larva is able to feed (Fig. 114). Other similar hydra-like larvæ

bud from its walls. How the medusæ arise from these larvæ is not known, but it seems probable that a direct change from the hydroid form to the medusa occurs.

The physiological processes of *Gonionemus* are very similar to those of *Hydra*. Food is captured while the animal is swimming, with the aid of nematocysts, and conveyed to the mouth by the tentacles, or the *Gonionemus* lies with its aboral surface up, and

any food that drops on its tentacles or manubrium are similarly engulfed.

#### (4) OTHER HYDROZOA

The members of this class are almost all colonial, and typical species exist as polyps which give rise by budding to free or sessile medusæ. The medusæ possess a velum and a nerve ring. There are no mesenteries nor stomodæum; the tentacles are usually solid; and the reproductive cells are ectodermal and discharged directly to the exterior. Four orders and a number of suborders are included here.

**Order 1. LEPTOLINA.** — HYDROZOA with an attached hydroid stage.

**Suborder 1. ANTHOMEDUSÆ (GYMNOBLASTEÆ).** — Perisarc usually covering cœnosarc but not the polyps and reproductive individuals; medusæ with gonads on the manubrium and with eyes.

*Hydra* lives in fresh water; is solitary; has 4 to 12 hollow tentacles; perisarc absent; no medusa. The species of *Hydra* that occur in North America, except *H. oligactis*, do not have the column differentiated into proximal stalk and distal body

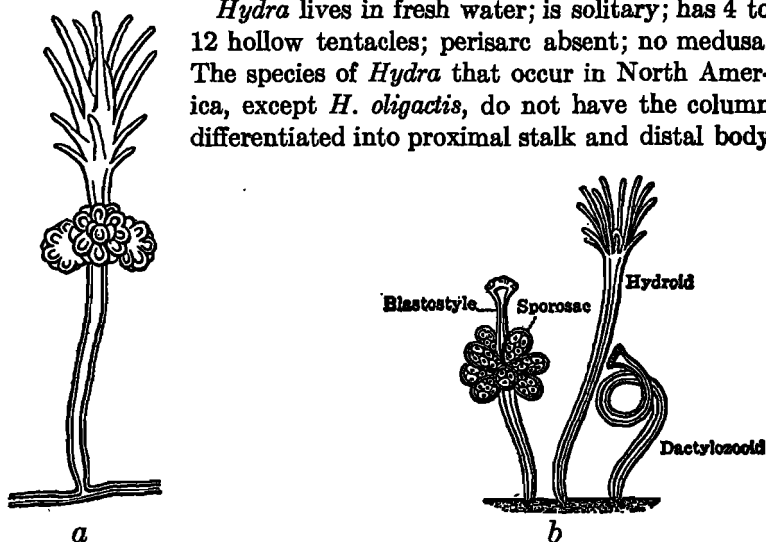


FIG. 115. — ANTHOMEDUSÆ. a, *Clava*; a hydroid bearing sporosacs. b, *Hydractinia*; four types of individuals. (After Allman, from Fowler.)

and are not dicecious but hermaphroditic, and the testes are located in the distal third of the body. *H. (viridis) viridissima* is green in color; *H. (grisea) vulgaris* is pale yellow, gray, or brown; *H. polypus* is gray or brown; *H. carnea* is reddish-brown; and *H. americana* is commonly white.



*Clava* (Fig. 115, a) forms a non-branching colony; the polyps rise from a filiform hydrorhiza and the tentacles are scattered irregularly over the hydranth; sporosacs are present at the base of the tentacles. *C. leptostyla* has reddish hydranths, about 20 tentacles, and pink (male) or purple (female) sporosacs; on *Fucus*, piles, etc.; Long Island northward.

*Bougainvillia* (Fig. 116, a) forms an arborescent colony; the hydranths possess a single whorl of filiform tentacles; the free-swimming medusa has four clusters of tentacles. *B. carolinensis* is about 10 cm. high with prom-

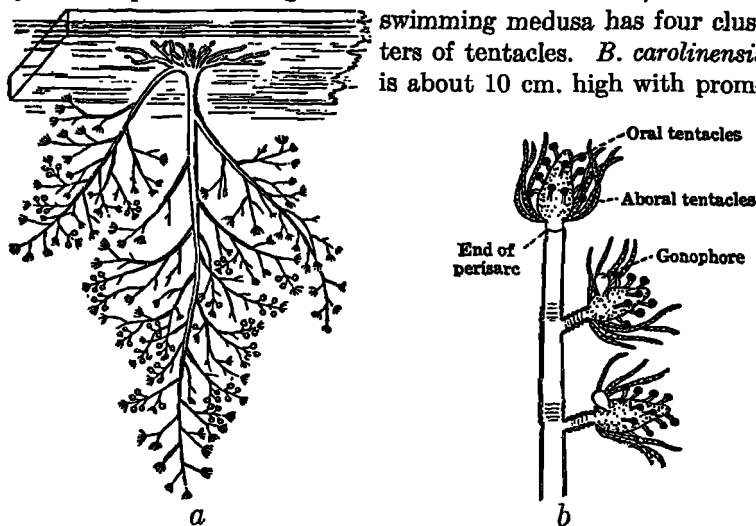


FIG. 116. — ANTHOMEDUSÆ. a, *Bougainvillia*; colony, natural size, hanging from floating object. b, *Pennaria*; tip of a branch. (a, after Allman; b, after Borradaile.)

inent hypostome and 12 tentacles; the medusa is about 4 mm. in diameter; on *Fucus*, piles, etc.; Cape Cod southward.

*Eudendrium* forms a branching colony; the polyps rise from a reticulated hydrorhiza; the hypostome is trumpet-shaped and has a single whorl of filiform tentacles; no medusæ but sporosacs present. *E. ramosum* forms large colonies about 12 cm. high; about 20 tentacles; sporosacs red (male) or orange (female); on rocks, piles, etc.; North Carolina northward.

*Hydractinia* (Fig. 115, b) forms an encrusting colony; the polyps are nutritive, reproductive, or defensive in function; no medusæ. *H. echinata* forms a colony about 10 mm. high; no tentacles are present on the reproductive polyps; on *Fucus*, rocks, piles, hermit crab shells, etc.; Atlantic coast.

*Podocoryne* resembles *Hydractinia* but has a medusa with 8 or more long tentacles. *P. fulgur* has a medusa about 1 mm. high and 4 oral and 8 marginal tentacles; may be phosphorescent; Massachusetts to North Carolina.

*Pennaria* (Fig. 116, b) forms a regularly branching colony; the hydranth possesses 10 to 12 filiform basal tentacles and knobbed

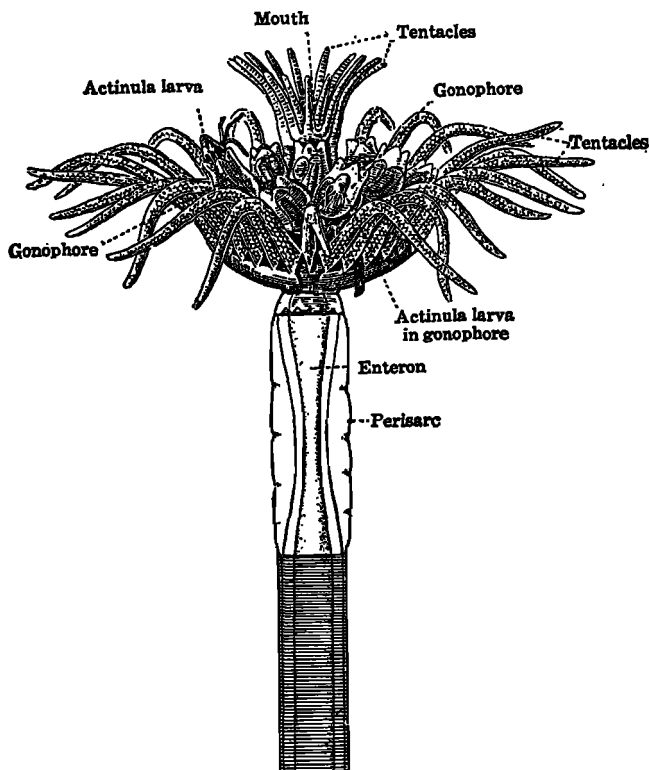


FIG. 117. — HYDROZOA. *Tubularia*. A single hydranth with medusoid individuals (gonophores) budded out between the two circles of tentacles. (After Allman.)

tentacles on the hypostome; medusa either sessile or free. *P. tiarella* is about 12 cm. high; bright pink in color; medusæ buds on side of hydranth, sessile or free; on rocks, piles, etc.; Maine southward.

*Tubularia* (Fig. 117) is solitary or forms large, pink colonies; the hydranth has one basal and one distal whorl or filiform tentacles; medusæ attached to polyp; free-swimming, hydroid-like

bodies are formed by medusoids. *T. crocea* forms dense tuft-like colonies about 9 cm. high; with 20 to 24 basal tentacles; on piles, etc.; Massachusetts southward.

**Suborder 2. LEPTOMEDUSÆ (CALYPTOBLASTEÆ).** — Perisarc covering cœnosarc and becoming hydrothecæ over nutritive

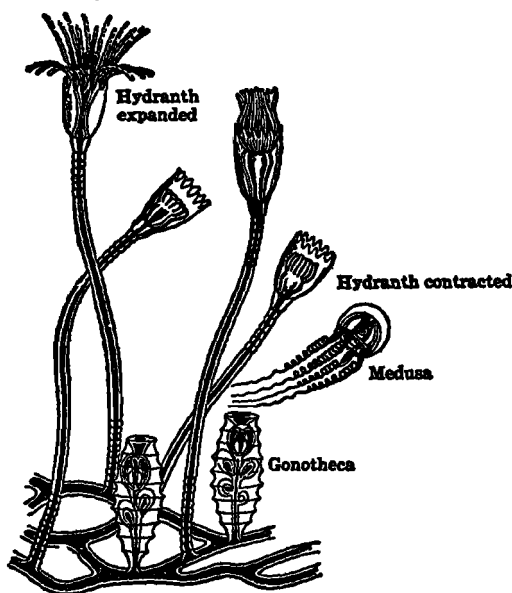


FIG. 118. — LEPTOMEDUSÆ. *Campanularia*. A colony with three types of individuals. (After Allman.)

polyps and gonothecæ over reproductive polyps; medusæ with gonads on the radial canals; usually statocysts.

*Obelia* (p. 65) and *Gonionemus* (p. 67) have already been described in detail.

*Sertularia* has opposing pairs of hydrothecæ along the stem; not joined to the stem by a stalk. *S. pumila* forms a branched colony about 3 cm. high; gonangia oval; on *Fucus*, etc.; New Jersey northward.

*Campanularia* (Fig. 118) forms a simple or branched colony; hydrothecæ bell-shaped and without operculum. *C. flexuosa* forms an irregularly branched colony about 25 mm. high; stem annulated near base of branches; stalks of hydrothecæ annulated; on piles, etc.; Long Island northward.

*Craspedacusta* lives in fresh water; has a small hydroid stage free from tentacles; medusa disk-shaped and with 4 radial canals; tentacles up to 300 or more in four size-groups; lithocysts up to 200 or more; manubrium long. *C. ryderi* has been recorded from several lakes and ponds in the United States but appears to be rare.

**Order 2. TRACHYLINA.** — HYDROZOA without alternation of generations; medusæ develop directly from eggs; tentaculocysts present; gonads on radial canals or on floor of gastric cavity.

**Suborder 1. TRACHYMEDUSÆ.** — Marginal tentacles on edge of umbrella; gonads on radial canals; sense tentacles in pits or vesicles.

*Liriope* (Fig. 119, A) is hemispherical and has a long manubrium and 6 or 8 closed lithocysts. *L. exigua* is about 2 cm. in diameter; Gulf Stream, New England.

*Aglantha* has 8 radial canals, 8 gonads on the radial canals and free lithocysts. *A. digitale* is about 3 cm. high and 1.5 cm. in diameter; many tentacles; gonads long; North Atlantic.

**Suborder 2. NARCOMEDUSÆ.** — Marginal tentacles aboral from edge of umbrella; gonads on oral wall of stomach; sense tentacles not enclosed.

*Cunina* is rather flat and transparent; the larvæ live as parasites within the umbrella of the mother or other medusæ. *C. lativentris* is about 1.5 cm. in diameter; 10 to 12 marginal lobes, tentacles

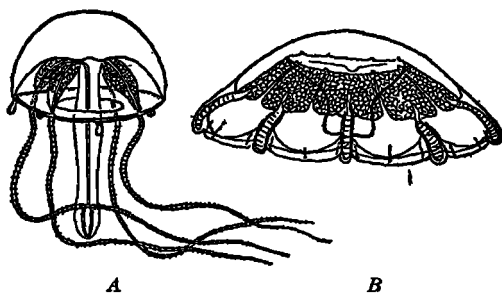


FIG. 119. — A, TRACHYMEDUSÆ. *Liriope scutigera*. B, NARCOMEDUSÆ. *Cunocanthia octonaria*. (A, after Fewkes; B, after Brooks.)

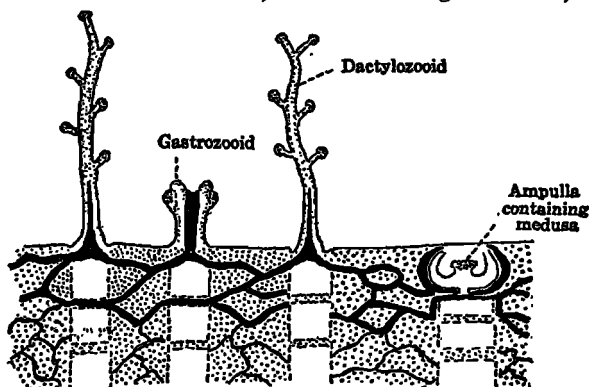


FIG. 120 — HYDROCORALLINA. *Millepora*. Diagrammatic section. Living canals shown in black; degenerating canals, by lines; skeleton by stippling. (From Borradaile and Potts, after Hickson.)

and gastric pouches; 4 lithocysts on each lobe; Atlantic and Mediterranean.

*Cunoclantha* (Fig. 119, B) has 8 marginal lobes, tentacles and gastric pouches; larvæ parasitic as in *Cunina*; larvæ produce larvæ by budding, *C. octonaria* is about 7 mm. in diameter; cosmopolitan.



FIG. 121. — SIPHONOPHORA. *Physalia*, the Portuguese man-of-war capturing a fish. (After Newman.)

**Order 3. HYDROCORALLINA.** — HYDROZOA with branched hydrorhiza; calcareous exoskeleton, branching, encrusting, or massive; polyps of two types, nutritive (gastrozooids) and for capturing prey (dactylozooids), arising from skeletal pits; medusoids from buds of the cœnosarc, mostly confined to skeletal pits (ampullæ); usually associated with reef corals in the tropics.

*Millepora* (Fig. 120) forms a massive base from which irregular branches arise; polyps very contractile; gastrozooids with 4 or 5 knobbed tentacles; dactylozooids bear tentacles; each gastrozoid surrounded by 5 or 6 dactylozooids; medusa simple, with 4 or 5 rudimentary tentacles.

*M. alcornis* lives on the

Florida coast; it is sometimes called the stinging coral because of its powerful nematocysts.

**Order 4. SIPHONOPHORA.** — Pelagic, colonial HYDROZOA highly polymorphic; the members of the colony bud off from a cœnosarc that arises from a planula larva. The following modifications may occur (Fig. 141):

(1) *Pneumatophore*: a sac filled with gas secreted by the epithelium; serves as a float.

(2) *Hydrophyllium*: finger-shaped or triangular; shields other members of colony

(3) *Nectocalyx*: a bell-shaped, modified medusa; propels colony through water.

(4) *Gastrozoid*: tubular or sac-shaped, with mouth; ingestion and digestion of food.

(5) *Dactylozoid*: long, tentacular; armed with many powerful nematocysts; defends colony and captures prey.

(6) *Gonozoid*: bell-shaped; resembles sexual medusa of ANTHOMEDUSÆ; produces ova or spermatozoa.

*Physalia* (Fig. 121) has a bladder-like pneumatophore with a dorsal crest up to 12 cm. in length that may contract forcing out the gas through a dorsal pore and thus bringing about submergence; a fresh supply of gas may be excreted bringing the colony to the

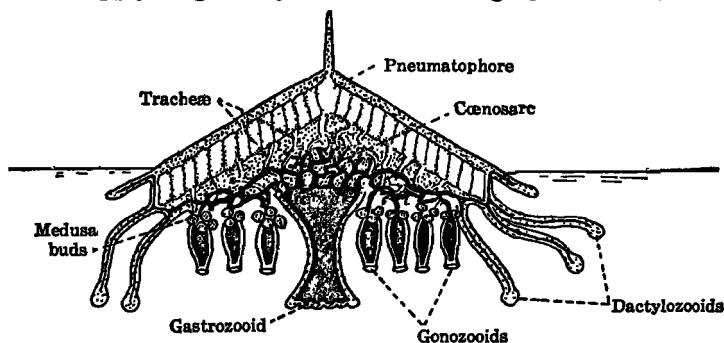


FIG. 122. — SIPHONOPHORA. *Velella*. Vertical section. The cavity of the pneumatophore is in white; the network of endodermal tubes, in black. (After Haeckel, modified.)

surface again. There are no nectocalyces, movement from place to place being due to currents in the water or winds against the pneumatophore. *P. pelagica*, the Portuguese man-of-war, has stinging dactylozooids up to 45 feet long; it occurs in the Gulf Stream from Florida northward; specimens are often cast up on the shores. The dactylozooids are able to catch large fish, which, by contraction, they draw up to the gastrozooids; these enclose the prey in a digestive sac by spreading their lips over it. The dactylozooids are able to contract to one seventieth of their maximum length. They exhibit rhythmic contraction waves, neuromuscular in nature, that travel at an average rate of 121 mm. per second.

*Velella* (Fig. 122) forms a colony that resembles a single medusa in appearance. The pneumatophore is a chambered disk from the

center of the ventral surface of which hangs a single large gastrozooïd surrounded by gonozooïds, with a circlet of dactylozooïds around the outer edge. Free medusæ arise from the gonozooïds. *V. mutica* has a pneumatophore about 4 cm. long with an elevated ridge on the dorsal surface that serves as a sail; it occurs on the Atlantic coast, especially southward.

## 2. CLASS II. SCYPHOZOA

### (1) AURELIA — A SCYPHOZOAN MEDUSA

*Aurelia* (Fig. 123) is one of the commonest of the scyphozoan jellyfishes. The species *A. flavidula* ranges from the coast of Maine

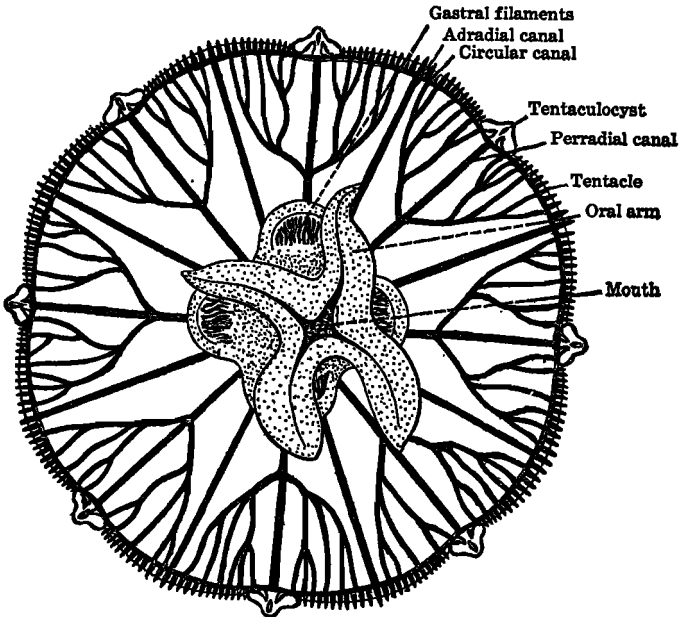


FIG. 123. — SCYPHOZOA. *Aurelia aurita*. Ventral view. (After Shipley and MacBride, modified.)

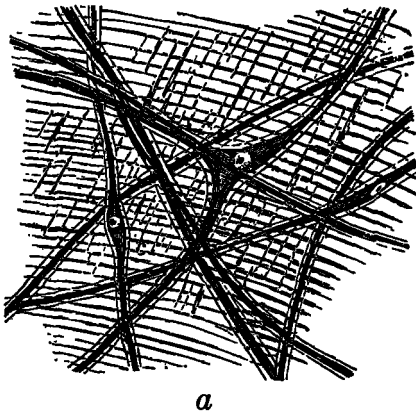
to Florida. Members of the genus may be recognized by the eight shallow lobes of the umbrella margin, and the fringe of many small tentacles.

In structure *Aurelia* differs from *Gonionemus* and other hydrozoan medusæ in the absence of a velum, the characteristics of the

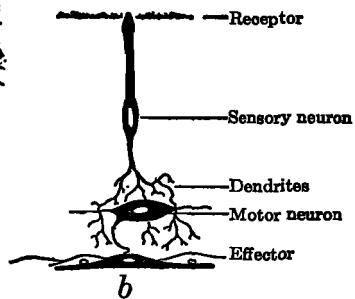
canal system, the position of the gonads, and the arrangement and morphology of the sense organs.

The *oral lobes* or *lips* of *Aurelia*, which hang down from the square mouth, are long and narrow, with folded margins. The *mouth* opens into a short *gullet*, which leads to the somewhat rectangular "*stomach*." A

*gastric pouch* extends laterally from each side of the stomach. Within each gastric pouch is a *gonad* and a row of small *gastric filaments* bearing *nematocysts*. Numerous *radial canals*, some of which branch several times, lead from the stomach to a *circumferential canal* at the margin.



a



b

FIG. 125. — *Aurelia aurita*; nerve cells. a, Scattered nerve-ganglion cells from subumbrella. b, Diagram of receptor-effector system. (a, after Schäfer; b, after Parker.)

The circulation of fluid within the canals is due to the beating of cilia attached to the endoderm cells (Fig. 124, a); is definite in

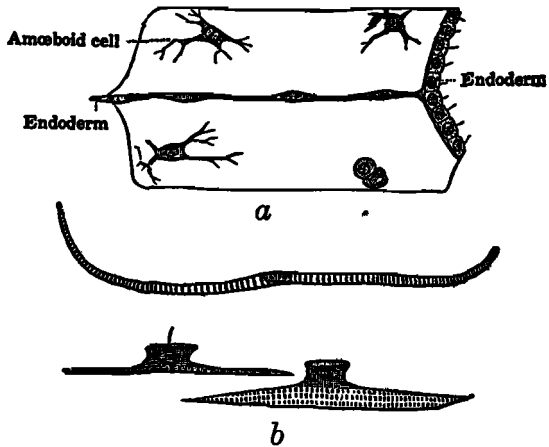


FIG. 124. — Histology of medusæ. a, *Aurelia*; section showing wandering cells, endoderm cells and mesoglea. b, *Lizzia*; above, muscular cell from subumbrella; below, two epithelio-muscular cells from base of tentacle. (After Hertwig, from Lankester.)



direction; and occupies a period of about 20 minutes. Water flows through the mouth into the gastric cavity; thence into the gastric

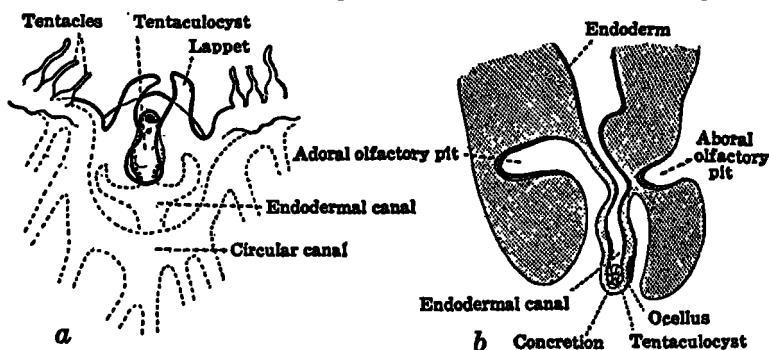


FIG. 126. — *Aurelia aurita*; tentaculocyst. a, Oral aspect. b, Longitudinal section. (a, after Fowler; b, after Eimer, from Fowler.)

pouches; through the adradial canals to the circular canal; into the interradial and perradial canals and out of exhalent grooves

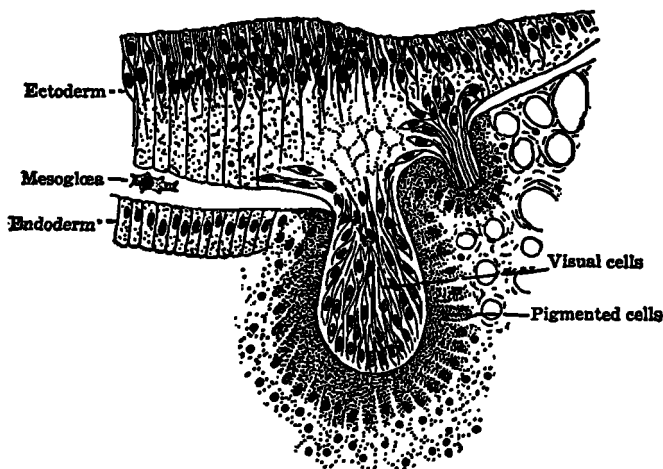


FIG. 127. — *Aurelia aurita*: section of double eye. (After Schewiakoff, from Dahlgren and Kepner.)

on the oral arms. Food particles carried by the circulatory fluid are engulfed by endoderm cells.

The ectodermal cells are more highly specialized for contraction than those of *Hydra* or *Gonionemus*; their bases are elongated into a cross-striated fiber capable of rapid rhythmic contraction

(Fig. 124, *b*). An ectodermal nerve net more complex than that of *Hydra* is also present (Fig. 125, *a*). A simple receptor-effector system exists in certain medusæ similar to that illustrated in figure 125, *b*. It consists of a receptor at the body surface ending in a nerve net which is associated with a nerve cell and thence with a muscle cell (effector).

The eight *sense organs* of *Aurelia* lie between the marginal lappets (Figs. 123, 126) and are known as *tentaculocysts*. They are considered to be organs of *equilibrium*. As shown in figure 126, each

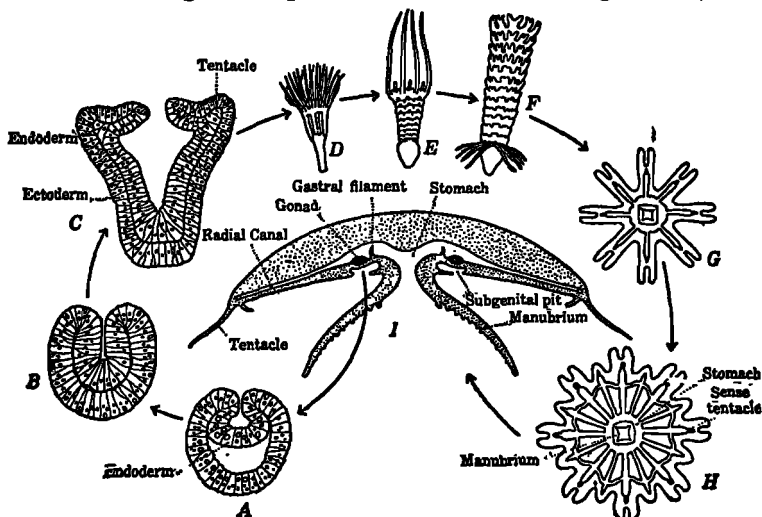


FIG. 128. — *Aurelia*: life-history. A, B, C, longitudinal sections through gastrula stages; D, scyphistoma; E, F, strobila; G, H, ephyra; I, vertical section through adult. (A, B, and C are more highly magnified than the other figures.) (From Kerr.)

tentaculocyst is a hollow projection connected with the endodermal canal. It contains a number of calcareous concretions formed by the endoderm, and bears an ectodermal pigment spot, the *ocellus* (Fig. 127), which is sensitive to light. The tentaculocyst is protected by an aboral hood and by lateral lappets. *Olfactory pits* are situated near by.

The gonads are frill-like organs lying in the floor of the gastric pouches. They have a pinkish hue in the living animal. The eggs or spermatozoa pass through the stomach and out of the mouth. An *alternation of generations* occurs in *Aurelia*, but the hydroid stage is subordinate. The eggs develop into free-swimming plan-

ulæ which become attached to some object and produce hydra-like structures, each of which is called a *hydra-tuba* (Fig. 128). This buds like *Hydra* during most of the year, but finally a peculiar process called *strobilization* takes place. The hydra-tuba divides into disks which cause it to resemble a pile of saucers; at this stage it is known as a *strobila*. Each disk develops tentacles, and, separating from those below it, swims away as a minute medusa called an *ephyra*. The ephyra gradually develops into an adult jellyfish.

## (2) OTHER SCYPHOZOA

Most of the larger jellyfishes belong to the SCYPHOZOA. They can be distinguished easily from the hydrozoan medusæ by the

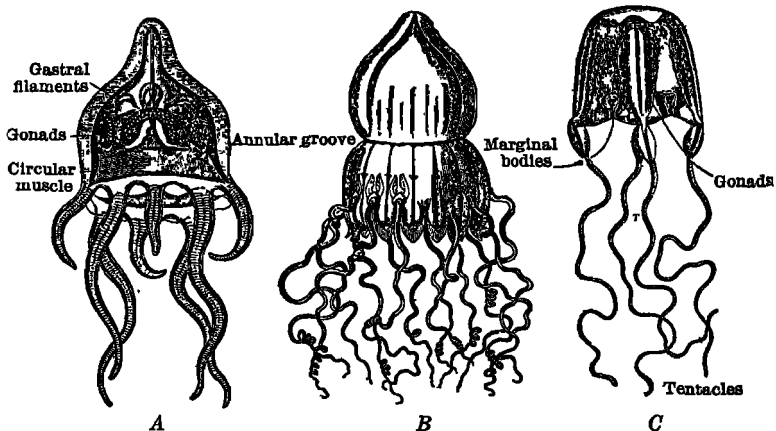


FIG. 129. — SCYPHOZOA. A, Order STAUROMEDUSÆ: *Tercera princeps*. B, Order PEROMEDUSÆ: *Periphylla hyacinthina*. C, Order CUBOMEDUSÆ: *Charybdea marsupialis*. (From Sedgwick, after Haeckel.)

presence of notches, usually 8 in number, in the margin of the umbrella. They are called acraspedote (without velum or craspedon) medusæ in contrast to the craspedote (with velum or craspedon) medusæ of the HYDROZOA. The SCYPHOZOA usually range from an inch to 3 or 4 feet in diameter, but some have been reported over 6 feet in diameter with tentacles over 40 feet long. They are usually found floating near the surface of the sea, though some of them are attached to rocks and weeds. There is an alternation of generations in their life history, but the asexual stage (the scyphistoma, Fig. 128, D) is subordinate. The class contains 4 orders.

**Order 1. STAUMEDUSÆ** (Fig. 129, A). — SCYPHOZOA without tentaculocysts; tentacles perradial and interrarial; umbrella goblet-shaped, temporarily attached by a narrow stalk at aboral pole; a stomodæum is present, suspended by four mesenteries; no alternation of generations.

*Lucernaria* has no statorhabs (adhesive pads) between the 8 lobes; stalk cylindrical. *L. quadricornis* is about 7 cm. high and 5 cm. in diameter; red, gray, or green in color; 100 or more tentacles on each lobe; Massachusetts northward, Europe.

*Haliclystus* has a margin with 8 lobes bearing many knobbed tentacles and eight statorhabs between the lobes; stalk quadrate. *H. auricular* is about 3 cm. high and 3 cm. in diameter; 100 or more tentacles on each lobe; Massachusetts northward, Alaska, Europe.

**Order 2. PEROMEDUSÆ.** — SCYPHOZOA with four interrarial tentaculocysts; tentacles perradial and adradial; umbrella conical, with transverse constriction; a stomodæum is present suspended by four mesenteries; no alternation of generations.

*Periphylla* has 16 marginal lobes, 12 tentacles, and horseshoe-shaped gonads. *P. hyacinthina* (Fig. 129, B) is about 8 cm. high and 4 cm. in diameter; reddish in color; cosmopolitan.

**Order 3. CUBOMEDUSÆ.** — SCYPHOZOA with four perradial tentaculocysts; tentacles interrarial; umbrella four-sided, cup-shaped; no alternation of generations.

*Charybdea* (Fig. 129, C) has a bell from 2 to 23 cm. high and 4 interrarial tentacles. *C. xycmacana* is transparent; lives in shallow water; is an active swimmer and a voracious feeder, ingesting comparatively large fish.

**Order 4. DISCOMEDUSÆ.** — SCYPHOZOA with four or more perradial and four or more interrarial tentaculocysts; umbrella disk-shaped; alternation of generations. This order contains most of the SCYPHOZOA.

*Aurelia* has already been described in detail (p. 76).

*Dactylometra* has a quadrate mouth with 4 long, oral lobes, 40 hollow marginal tentacles, 48 marginal lobes, and 8 tentaculocysts. *D. quinquecirrha*, the common sea nettle, reaches a diameter of 25 cm.; Long Island southward.

*Cyanea* is a large disk-shaped medusa with no margins but 8 groups of very long tentacles on the subumbrella; long, large oral lobes. *C. capillata* is our largest jellyfish ranging from 10 cm. to

2 meters in diameter and possessing tentacles over 40 feet long; North Carolina northward.

### 3. CLASS III. ANTHOZOA

#### (1) METRIDIDIUM — A SEA-ANEMONE

*Metridium marginatum* (Fig. 130) is a sea-anemone which fastens itself to the piles of wharves and to solid objects in tidepools along the North Atlantic coast. It is a cylindrical animal with a crown of hollow *tentacles* arranged in a number of circlets about the slit-

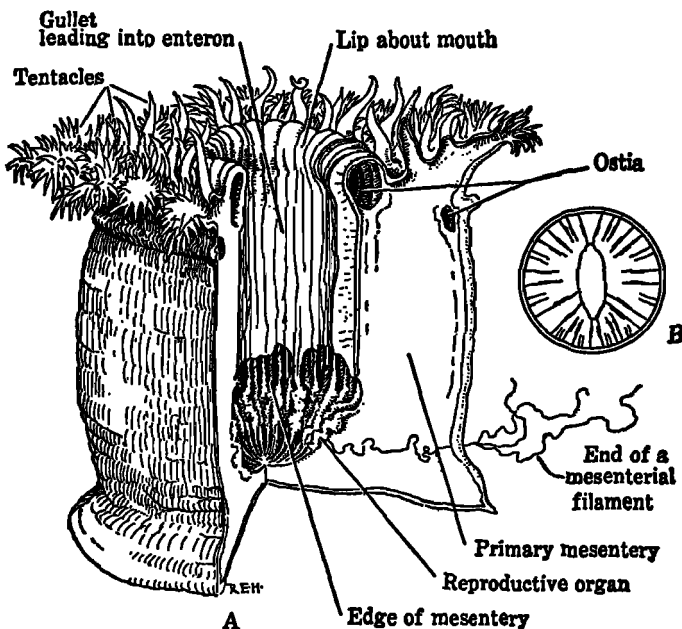


FIG. 130. — *Metridium marginatum*. View of a specimen with one quadrant removed. (From Woodruff.)

like *mouth*. The tentacles as well as the body can be expanded and contracted, and the animal's position may be changed by a sort of creeping movement of its *basal disk*. The *skin* is soft but tough and contains no skeletal structures. The tentacles capture small organisms by means of *nematocysts*, and carry the food thus obtained into the mouth. The beating of the *cilia* which cover the tentacles and part of the mouth and *gullet* is necessary to

force the food into the *gastrovascular cavity*. At either side of the gullet, or *stomodæum*, is a ciliated groove called the *siphonoglyph*. Usually only one or two siphonoglyphs are present, but sometimes three occur in a single specimen. A continual stream of water is carried into the body cavity through these siphonoglyphs, thus maintaining a constant supply of oxygenated water.

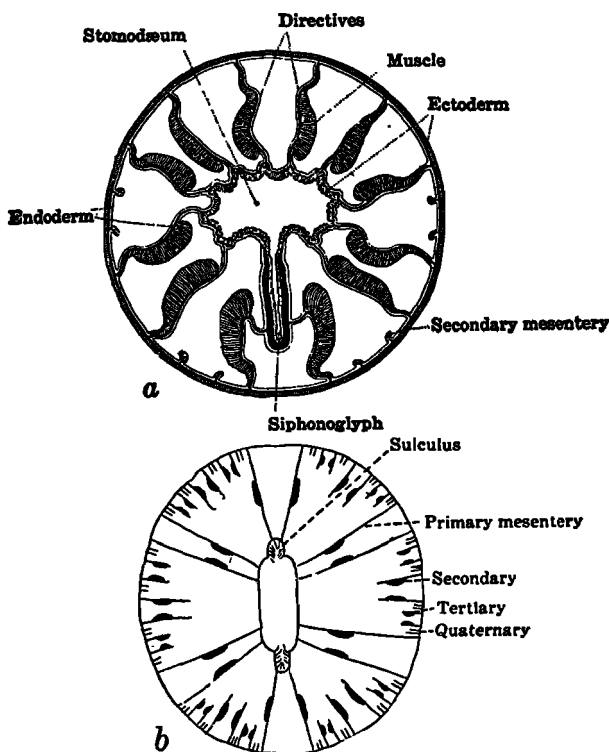


FIG. 131. — Mesenteries of sea-anemonies as seen in transverse sections. a, Section through stomodæum of *Peachia*. b, Section through typical actinian. (a, from Kerr; b, from Borradaile and Potts.)

If a sea-anemone is dissected, the central or *gastrovascular* (*coelenteric*) cavity will be found to consist of six radial chambers; these lie between the gullet or stomodæum and the body wall, and open into a common basal cavity. The six pairs of thin, double partitions between these chambers are called *primary septa* or *mesenteries* (Fig. 131). Water passes from one chamber to another through pores (*ostia*) in these mesenteries. Smaller

mesenteries project out from the body wall into the chambers, but do not reach the stomodæum; these are *secondary mesenteries*. *Tertiary mesenteries* and *quarternary mesenteries* lie between the primaries and secondaries. There is considerable variation in the number, position, and size of the mesenteries.

Each mesentery possesses a longitudinal retractor *muscle band*. The bands of the pairs of mesenteries face each other except those of the primaries opposite the siphonoglyphs. These primaries, which are called *directives*, have the muscle bands on their outer surfaces. The edges of the mesenteries below the stomodæum are provided with *mesenteric filaments* having a secretory function. Near the base these filaments bear long, delicate threads called *acontia*. The acontia are armed with *gland cells* and *nematocysts*,

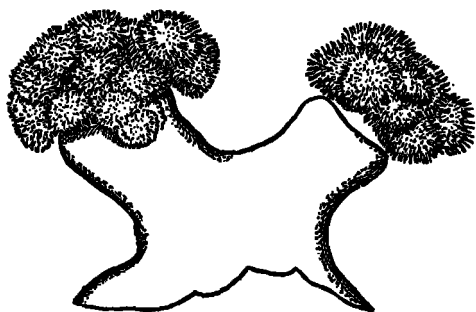


FIG. 132. — *Metridium*. A stage in binary fission. (After Agassiz and Parker.)

and can be protruded from the mouth or through minute pores (cinclides) in the body wall. They probably serve as organs of offense and defense.

Near the edge of the mesenteries lying parallel to the mesenteric filaments are the *gonads*.

The animals are *dicocious*, and the eggs or spermatozoa are shed into the gastrovascular cavity and pass out through the mouth. The fertilized egg probably develops as in other sea-anemones, forming first a free-swimming planula and then, after attaching itself to some object, assuming the shape and structure of the adult.

*Asexual reproduction* is of common occurrence, new anemones being formed by *budding* or *fragmentation* at the edge of the basal disk. *Longitudinal fission* has also been reported (Fig. 132).

## (2) ASTRANGIA — A CORAL POLYP

*Astrangia danzæ* (Fig. 133) is a coral polyp inhabiting the waters of our North Atlantic coast. A number of individuals live together in colonies attached to rocks near the shore. Each polyp looks like a small sea-anemone, being cylindrical in shape and possessing a crown of tentacles. The most noticeable difference is the

presence of a basal cup of calcium carbonate termed the *theca* (Fig. 134). This structure of calcium carbonate is what we commonly call coral. It is produced by the ectoderm of the coral polyp and increases gradually during the life of the animal.

The *calcareous cup* is divided into chambers by a number of radial *septa* which are built up between the pairs of mesenteries of the polyp. The center of the cup is occupied by a *columella* formed in part by the fusion of the inner ends of septa, and in part by projections from the base of the polyp. Although *Astrangia* builds a cup less than half an inch in height, it produces enormous masses of coral in the course of centuries.

The food of *Astrangia* consists of small organisms, such as algæ, PROTOZOA, hydroids, worms, crustaceans, and mollusks. These organisms are ingested as a result of the muscular action of the

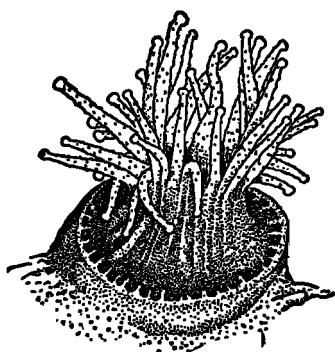


FIG. 133. — *Astrangia*. A specimen with tentacles extended from the theca. (From Johnson and Snook.)

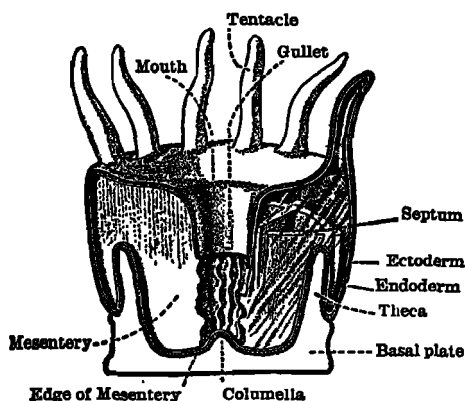


FIG. 134. — Semi-diagrammatic view of one-half of a simple coral polyp. (From Shipley and MacBride.)

tentacles and central part of the oral disk. The mucus secreted by the oral disk and cilia of the stomodæum also play a part in ingestion. A trypsin-like enzyme of digestive value is probably secreted into the gastrovascular cavity, but the principal method of digestion is intracellular. Food particles are engulfed by the mesenterial filaments in which food vacuoles are formed.

The reaction of these vacuoles is at first acid but changes to alkaline after about two days. Digestion probably occurs during the period of alkalinity. Some specimens contain zooxanthellæ



and those that do not may easily be infected if they are fed on crab meat mixed with parts of the tissues of heavily infected polyps. Infected polyps use these zooxanthellæ as food, digesting them in their mesenteric filaments.

### (3) OTHER ANTHOZOA

The ANTHOZOA or ACTINOZOA are solitary or colonial coelenterates with a polyp stage but no medusæ. The polyps have a coelenteron divided into chambers by radially arranged membranes known as mesenteries. A stomodæum is present. Most of the ANTHOZOA secrete a calcareous skeleton which we know as coral. Two subclasses with three orders in each are presented in the following discussion.

**SUBCLASS I. ZOANTHARIA.** — ANTHOZOA with usually many simple hollow tentacles, arranged generally in multiples of five or six;

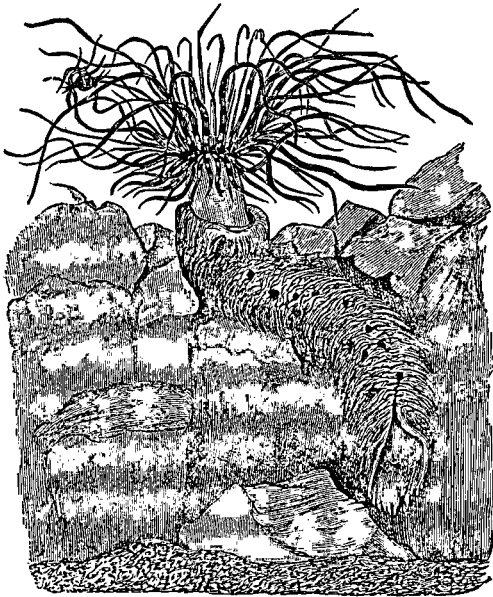


FIG. 135. — ACTINIARIA. *Cerianthus*, a solitary sea-anemone with many tentacles. (After Andres, from Hickson.)

two siphonoglyphs as a rule; mesenteries vary in number; skeleton absent or present; simple or colonial; dimorphism rare.

**Order 1. ACTINIARIA.** — ZOANTHARIA usually solitary; many complete mesenteries; no skeleton. These are the sea-anemones many of which are beautifully colored; in the large *Stoichactis* of the Great Barrier Reef of Australia, “the spheroidal bead-like tentacles occur in irregularly

mixed patches of gray, white, lilac, and emerald green, the disk being shaded with tints of gray, while the oral orifice is bordered with bright yellow.” (Kent.)

*Metridium* has already been described in detail (p. 182).

*Edwardsia* is a slender, solitary type of sea-anemone with 16 tentacles in 2 circlelets of 8 each. *E. leidyi* is about 3 cm. long and 1.5 mm. in diameter; it is parasitic on a ctenophore, *Mnemiopsis leidy* (p. 204).

*Cerianthus* (Fig. 135) is also solitary in habit; it possesses many tentacles in 2 rows and one siphonoglyph. The ectoderm



FIG. 136. — Corals on the Great Barrier Reef of Australia. (From Saville Kent.)

secretes a long tube of mucus in which the animal lives. *C. americanus* occurs from Cape Cod to Florida. It reaches a length of 60 cm. and is about 25 mm. in diameter. As many as 130 tentacles may be present.

*Halcompa* has a long, slender body consisting of three parts, a foot region, a central region usually covered with sand, and an oral retractile region; habitat, sand or mud. *H. farinacea* is about 2 cm. long and 3 mm. in diameter; 12 tentacles in two circlelets; Massachusetts northward.

*Sagartia* possesses a sphincter, acontia, and cinclides; 3 or 4 circlelets of retractile tentacles; surface smooth; oral disk not lobed. *S. luciae* is about 8 mm. long and 6 mm. in diameter; 4 rows

of tentacles, 84 in all; olive green in color with orange longitudinal stripes; Long Island northward.

**Order 2. MADREPORARIA** (Figs. 136, 137). — **ZOANTHARIA** usually colonial; many complete mesenteries; calcareous skeleton formed by ectoderm cells. Most of the stony corals belong to this order. Many of the coral polyps are tinted with pink, lilac, yellow,

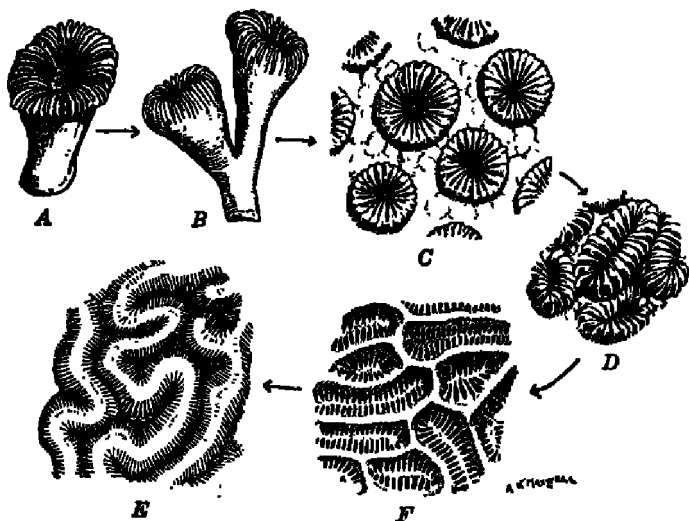


FIG. 137. — **ZOANTHARIA** The skeletons of various genera of corals. A, *Caryophyllia*; B, *Lophohelia*; C, *Solenastrea*; D, *Dichocenia*; E, *Favia*; F, *Meandrina*. (From Kerr.)

green, violet, red, etc., and give the coral reefs the wonderful color effects for which they are famous.

*Astrangia* has already been described (p. 184).

*Porites* forms a more or less branching porous colony with zooids close together; cup with 12 short septa. *P. porites* occurs in Florida and the West Indies.

*Oculina* forms a dendritic compact colony with zooids spirally arranged and widely separated. *O. diffusa* is much branched; cup 3 mm. in diameter; North Carolina to Florida.

*Meandrina* has confluent zooids with septa in rows. *M. sinuosa* forms massive, encrusting colonies up to 25 cm. or more in diameter and is known as brain coral; the sinuous ridges on the surface are septa and grooves; Florida and West Indies.

*Fungia* has no siphonoglyph; solitary; large; concave below and convex above. *F. elegans* is about 6 cm. in diameter; Gulf of California.

**Order 3. ANTIPATHIDEA.** — Colonial ZOANTHARIA with a horny, usually branching axial skeleton, but no calcareous spicules; in all the large seas, usually at a depth of from fifty to five hundred fathoms; black corals.

*Antipathes* forms branching colonies of long slender stalks; polyps with 6 tentacles. *A. larix* has an axis with many long spines; up to 3 feet long; 6 longitudinal rows of parallel branches from 3 to 10 cm. long along main stalk; West Indies, Mediterranean.

*Cirripathes* is unbranched. *C. spiralis* has a flexible spiral stalk over 3 feet long; West Indies, Mediterranean, Indian Ocean

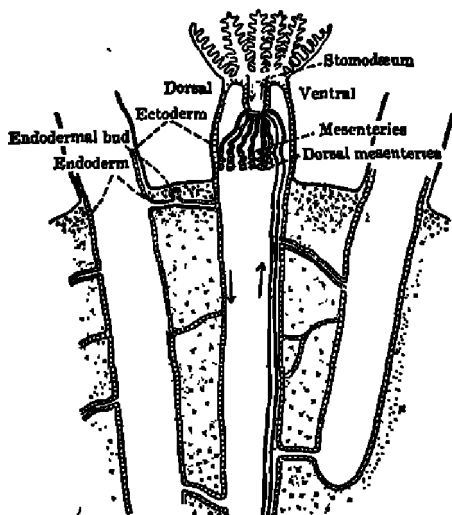


FIG. 138. — ALCYONARIA. *Alcyonium*. Diagram of section through colony showing extended polyps with pinnate tentacles and ctenosarc. The direction of water-circulation is shown by arrows. The mesoglea is indicated by dots and the spicules it contains by small crosses. (From Borradaile and Potts)

**SUBCLASS 2. ALCYONARIA.** — ANTHOZOA with 8 hollow, pinnate tentacles, and 8 complete mesenteries; with 1 siphonoglyph, ventral in position; and with the retractor muscles of the mesenteries all on the side toward the siphonoglyph.

**Order 1. ALCYONACEA.** — Colonial ALCYONARIA; zooids united into a compact mass by fusion of body walls (Fig. 139, a); skeleton of calcareous spicules which do not form a solid axial support.

*Alcyonium* (Fig. 138) forms a colony of thick, soft, leathery lobes; polyps long but all except distal end buried in the mesoglea (coenenchym). *A. carneum* is from 4 to 10 cm. high; yellow or red; Long Island northward.

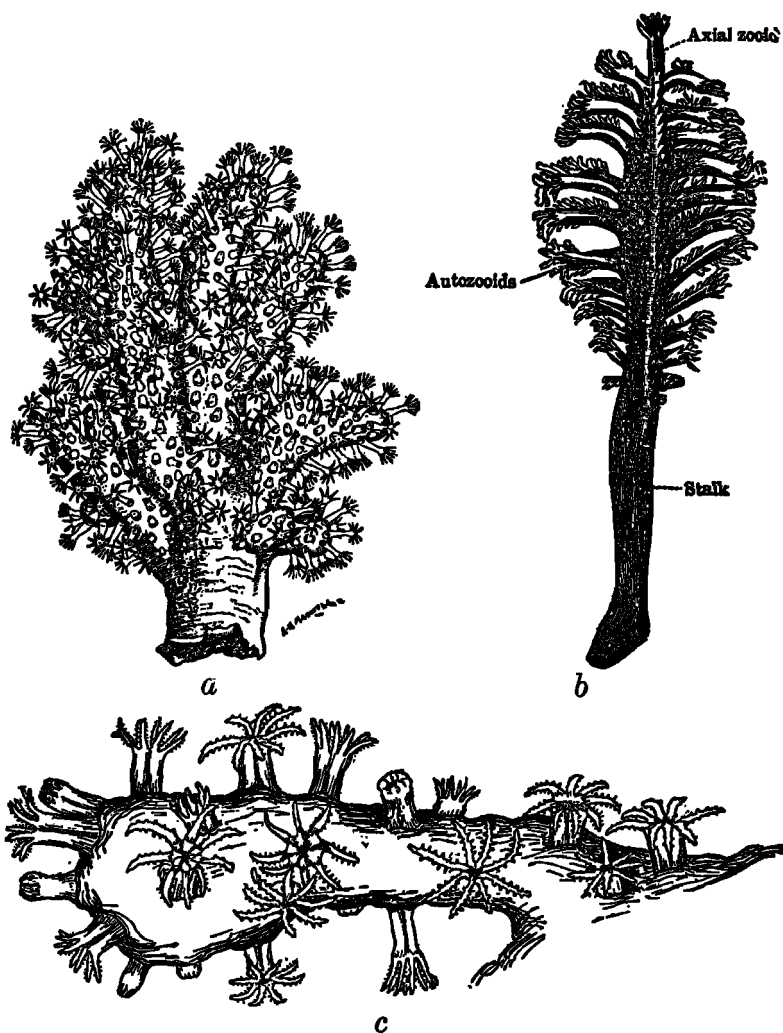


FIG. 139. — ALCYONARIA. a, ALCYONACEA. *Alcyonium palmatum*, with polyps extended. b, PENNATULACEA. *Pennatula*, a sea feather or sea pen. c, GORGONACEA. *Euplexaura marki*, with polyps extended. (a, from Kerr; b, after Jungerson; c, from Johnson and Snook.)

*Tubipora* has polyps joined together by horizontal bars. *T. musica* forms organ-pipe coral; tentacles bright green; skeleton dull red; on coral reefs in Old and New World.

**Order 2. GORGONACEA** (Fig. 139, c). — Colonial **ALCYONARIA**; skeletal axis branched and not perforated by gastrovascular cavities of the zooids.

*Corallium* forms the precious red coral of commerce; polyps retractile, white; axis hard, red. *C. nobile (rubrum)* is up to 30 cm. high; Mediterranean.

*Gorgonia* produces a fan-shaped colony in which the branches unite to form a network in one plane. *G. flabellum* is the sea fan; up to 50 cm. high and wide; yellow or red; West Indies, South Atlantic.

**Order 3. PENNATULACEA.** — **ALCYONARIA** forming bilaterally symmetrical colonies; zooids usually borne on branches of an axial stem, which is supported by a calcareous or horny skeleton; sea pens and sea feathers.

*Pennatula* (Fig. 139, b) is called a sea feather; stalk embedded in sand or mud; distal end of stalk (rachis) with paired lateral branches (pinnulæ). *P. aculeata* has from 20 to 50 long pinnulæ on each side; about 10 cm. long; red; South Carolina northward.

*Renilla* forms a circular or reniform (kidney-shaped) rachis; polyps all dorsal. *R. reniformis* has white polyps; dorsal surface of rachis pink or violet; about 7 cm. long; North and South Carolina, West Indies.

#### 4. CŒLEENTERATA IN GENERAL

**Morphology.** — The foregoing account has shown that cœlenterates all possess a body wall composed of two layers of cells, an outer ectoderm and an inner endoderm. They are, therefore, diploblastic, although many **ANTHOZOA** have a fairly well-developed mesoderm. Between these layers is a jelly-like non-cellular substance, the mesoglea. The body wall encloses a single cavity, the cœlenteron or gastrovascular cavity, in which both digestion and circulation take place. In some of the cœlenterates, like *Hydra* (Fig. 98), this cavity is simple, but in others, like *Aurelia* (Fig. 123), it is modified so as to include numerous pouches and branching canals.

So far as is known, all cœlenterates possess stinging cells called *nematocysts*; these are organs of offense and defense. *Muscle*

*fibrils* are present in a more or less concentrated condition (Fig. 124). *Nerve fibers* and *sensory organs* are characteristic structures; they may be few in number and scattered as in *Hydra* (Fig. 104), or numerous and concentrated as in *Aurelia* (Fig. 125).

*Hydroid and medusa compared.*—The two principal types of coelenterates are the polyp or hydroid, and the jellyfish or medusa. These are fundamentally similar in structure (Fig. 140), but are variously modified (Fig. 141). Both polyps and medusæ are radially symmetrical. Although the medusæ upon superficial ex-

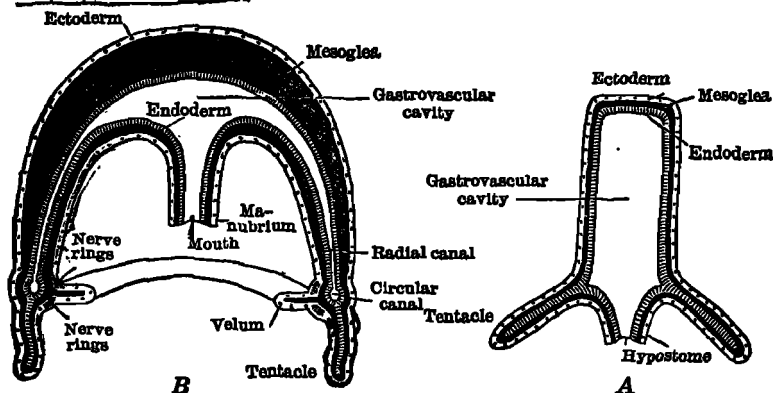


FIG. 140. — Diagrams showing the similarities of a polyp (A) and a medusa (B). (From Parker and Haswell.)

amination appear to be very different from the polyps or hydroids, they are constructed on the same general plan as the latter. Figure 140 illustrates in a diagrammatic fashion the resemblance between the hydrozoan polyp (A) and medusa (B) by means of longitudinal sections. If the medusa were grasped at the center of the aboral surface and elongated, a hydra-like form would result. Both have similar parts, the most noticeable difference being the enormous quantity of mesoglea present in the medusa.

*Metagenesis.*—Metagenesis is the alternation of a generation which reproduces only asexually by division or budding with a generation which reproduces only sexually by means of eggs and spermatozoa. This phenomenon occurs in other groups of the animal kingdom, but finds its best examples among the HYDROZOA. *Obelia* is an excellent illustration of a metagenetic animal. The asexual generation, the colony of polyps (Fig. 111), forms buds of two kinds, the hydranths and the gonangia. The medusæ (Fig.

112, a), or sexual generation, reproduce the colony by means of eggs and spermatozoa.

f. The polyp and medusa stages are not equally important in all HYDROZOA; for example, *Hydra* has no medusa stage and *Geryonia* no polyp or hydroid stage. Various conditions may be illustrated by different HYDROZOA. In the following list, O represents the fertilized ovum, H, a polyp, M, a medusa, m, an inconspicuous or degenerate medusa, and h, an inconspicuous or degenerate polyp.

1. O — H — O — H — O (*Hydra*).
2. H — m — O — H — m — O (*Sertularia*).
3. O — H — M — O — H — M — O (*Obelia*).
4. O — h — M — O — h — M — O (*Liriope*).
5. O — M — O — M — O (*Geryonia*).

**Polymorphism.** — The division of labor among the cells of a METAZOON has already been noted. When division of labor occurs among the members of a colony, the form of the individual is suited to the function it performs. A colony containing two kinds of members is said to be *dimorphic*; one containing more than two kinds, *polymorphic*. Some of the most remarkable cases of polymorphism occur among the HYDROZOA (see list, page 174). The "Portuguese man-of-war" (Fig. 121), for example, consists of a float with a sail-like crest from which a number of polyps hang down into the water. Some of these polyps are nutritive, others are tactile; some contain batteries of nematocysts, others are male reproductive zooids, and

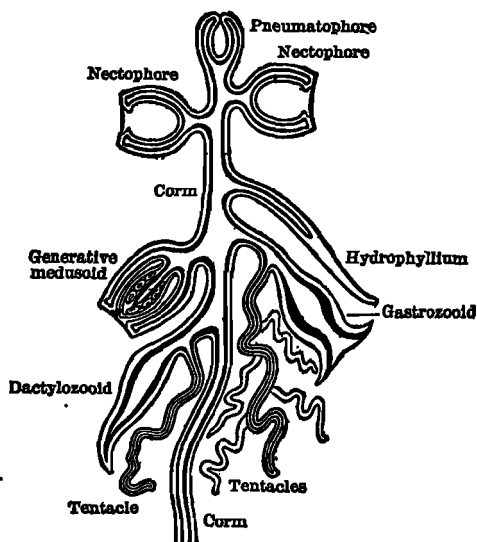


FIG. 141. — SIPHONOPHORA. Diagram showing possible modifications of medusoids and hydroids. The thick black line represents endoderm, the thinner line ectoderm. (After Allman.)

of these polyps are nutritive, others are tactile; some contain batteries of nematocysts, others are male reproductive zooids, and



still others give rise to egg-producing medusæ. The following tables indicate some of the modifications that may occur among the members of colonial HYDROZOA.

POLYMORPHIC MODIFICATIONS OF THE MEDUSOIDS OF THE HYDROZOA

NAME	STRUCTURE	FUNCTION
<u>Sexual medusoid</u>	Like typical medusa of ANTHOMEDUSÆ or modified because of arrested development	<u>Production of ova or spermatozoa.</u>
<u>Nectophore</u>	Without tentacles, manubrium, and mouth	<u>Locomotion</u>
Hydrophyllium	<u>Shield shaped</u>	<u>Protective</u>
✓Pneumatophore	<u>Air sac</u>	<u>Hydrostatic</u> ✓
Aurophore	Ovoid	Unknown

POLYMORPHIC MODIFICATIONS OF THE HYDROIDS OF THE HYDROZOA

NAME	STRUCTURE	FUNCTION
Gastrozooid	With <u>large mouth</u> , nematocysts, and <u>tentacle bearing nematocysts</u>	Ingestion of food
Dactylozooid	<u>Without mouth</u> ; with many nematocysts and tentacles	Offense and defense
Blastostyle	<u>Without mouth or tentacles</u>	<u>Produces sexual medusoids by budding</u>

**Physiology.** — The food of coelenterates consists principally of small, free-swimming animals, which are usually captured by means of nematocysts and carried into the mouth by tentacles and cilia. *Digestion* is mainly *extracellular*, enzymes being discharged into the gastrovascular cavities for this purpose. The digested food is transported to various parts of the body by currents in the gastrovascular cavity, and is then taken up by the endoderm cells and passed over to the ectoderm cells. Both *respiration* and *excretion* are performed by the general surface of the ectoderm and endoderm. *Motion* is made possible by muscle fibrils, and many species have also the power of *locomotion*. There is no true *skeleton*, although the stony masses built up by coral polyps support the soft tissues to a certain extent. The nervous tissue and sensory organs provide for the perception of various kinds of stimuli and the conduction of impulses from one part of the body to another. Coelenterates are generally sensitive to light inten-

sities, to changes in the temperature, to mechanical stimuli, to chemical stimuli, and to gravity. *Reproduction* is both asexual,

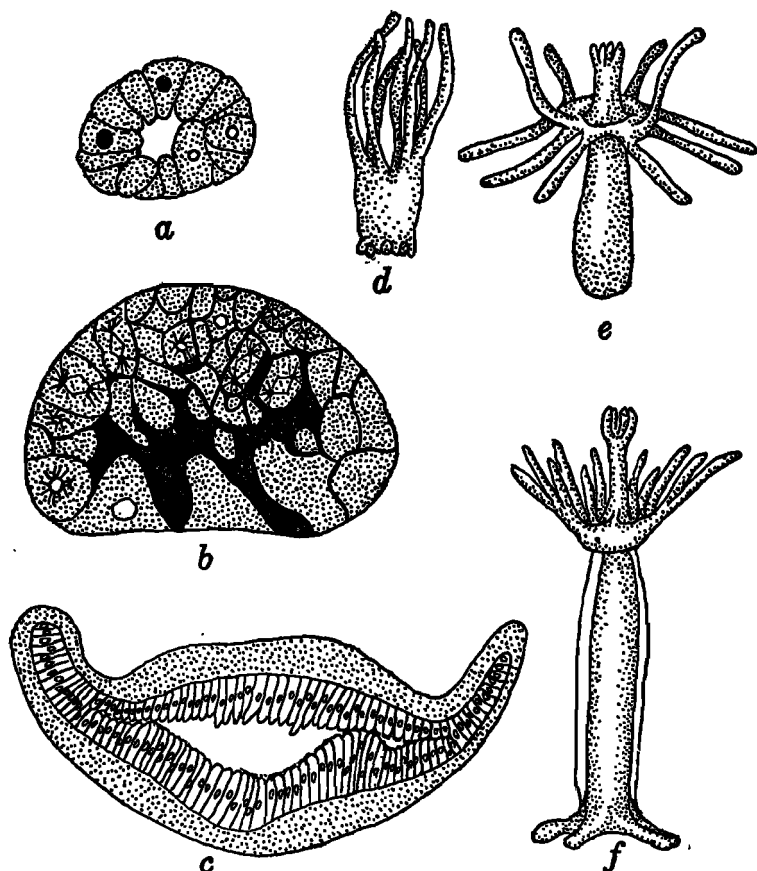


FIG. 142. — *Tubularia*. Stages in the embryology of a hydrozoan. a, Blastula. b, Endoderm cells budding off from wall of blastula. c, Formation of aboral tentacles. d, Aboral tentacles well developed; oral tentacles appearing. e, Larva in creeping stage. f, Larva at time of attachment to substratum. (a, b, c, after Brauer; d, e, f, after Allman.)

by budding and fission, and sexual, by means of eggs and spermatozoa.

*Asexual reproduction* is characteristic of some coelenterates and rare or absent in others. The most common method is by *budding*. The wall of the hydroid sends out a hollow protrusion which may become either a new hydroid or a medusa. Certain medusæ

also produce medusæ by budding. *Fission* is rare in hydroids and very rare in medusæ.

*Sexual reproduction.* — Both male and female germ cells are rarely developed by a single individual as in certain hydras. Usually a colony produces either ova or spermatozoa, or these originate in different individuals of a single colony. Sometimes one blastostyle may give rise to both kinds of germ cells.

*Embryology.* — *Tubularia* may be selected to illustrate the embryology of a hydrozoon (Fig. 142). Segmentation of the egg results in a hollow *blastula* of cells of different sizes. Cells are divided off from the wall into the cavity of the blastula until this cavity is completely filled. Spaces now appear among the inner mass of cells due to their absorption, and eventually a single central cavity results which is the *calenteron* or gastric cavity. The outer layer of cells of this *gastrula* is the *ectoderm* and the inner layer, the *endoderm*. The embryo now becomes disk-shaped and from the edge *aboral tentacles* grow out. Then the embryo elongates into a cylindrical form; a *mouth* opening appears in the center of the end opposite the aboral tentacles; and *oral tentacles* are pushed out around the mouth. This *actinula larva* (Fig. 117) escapes from the gonophore and sinks to the bottom where it becomes attached by the aboral end. It increases in length; *buds* appear at the sides; and creeping *stolons* grow out from the base. The latter give rise to upright shoots each of which produces daughters by lateral budding.

The embryology of a scyphozoon such as *Aurelia* (Fig. 128), differs considerably from that of *Tubularia*. The eggs of *Aurelia* undergo *cleavage* that results in the formation of a hollow, spherical *blastula*. This becomes invaginated into a *gastrula* with two layers of cells, an outer *ectoderm* and an inner *endoderm*, and with a central cavity, the *calenteron*, which communicates with the outside through a *blastopore*. The ectoderm becomes ciliated and the gastrula changes from spherical to oval in shape. After a free-swimming existence of four or five days the larva becomes attached at the aboral end and assumes a cup shape. A cone now arises with the blastopore in the center and four *primary tentacles* grow out around the blastopore which may now be called the *mouth*. These tentacles are solid, with a central core of endoderm covered by a layer of ectoderm. The larva changes gradually into the *hydra-tuba* or *scyphistoma* stage. Four *secondary tentacles* now grow out alternating with the primary tentacles; next eight more

tentacles develop and soon another set of eight all of which form a single circle of twenty-four tentacles around the mouth. Meanwhile *nematocysts* are formed in the ectoderm and groups of them appear like warts on the tentacles.

**Phylogeny.** — Speculation regarding the origin of the CŒLENTERATA and their differentiation into classes is a fascinating pastime. Embryology has led to "the following conception of the past history of the lower METAZOA. A widespread and dominant race of blastula-like animals once swarmed in the primeval seas. Some of these took a creeping life and eventually gave rise to the group of sponges; others kept to the free-swimming life and developed into planulæ, and so gave rise to the CŒLENTERATA. Some of these planulæ, by the specialization of the cilia into comb-like locomotor organs, became CTENOPHORA; whilst the remainder adopted a fixed life, and attached themselves by their aboral poles. This change occurred in different divisions of the stock at different stages of the evolution of the internal organs of the planula ancestor, and in this way the groups of HYDROZOA, SCYPHOZOA and ACTINOZOA arose." (MacBride.)

**The history of our knowledge of the Cœlenterata.** — The cœlenterates were originally called ZOOPHYTA or plant-animals. They were included by Cuvier, together with the ctenophores and echinoderms, in a division known as RADIATA, principally because of their radial symmetry. The study of echinoderm embryology proved these animals to be fundamentally bilaterally symmetrical, and a comparison of the anatomy of adult cœlenterates and echinoderms revealed the absence of a cœlom in the former, as well as many other profound differences. Leuckart in 1847 coined the term CŒLENTERATA for the group and elevated them to a distinct phylum. The term *polypus* we owe to Trembley who introduced the name in 1744 because *Hydra* resembles somewhat in appearance the octopus which was known to the ancients as the polyp. Linnæus and his predecessors called the jellyfish *medusæ* since their tentacles reminded them of the curls of *Medusa*. At first the cœlenterates and ctenophores were both included in the phylum CŒLENTERATA but the latter appear to be more closely related to the PLATYHELMINTHES than to the CŒLENTERATA and are now usually considered as a separate phylum.

**Relations of Cœlenterates to Man.** — Cœlenterates as a whole are of very little economic importance. They are probably very

seldom used as food by man but are eagerly devoured by fishes. Some corals are used as ornaments and for the manufacture of jewelry. Coral polyps build *fringing reefs*, *barrier reefs*, and *atolls* (Fig. 136). These occur where conditions are favorable, principally in tropical seas, the best known being among the Maldivé Islands of the Indian Ocean, the Fiji Islands of the South Pacific Ocean, the Great Barrier Reef of Australia, and in the Bahama Island region.

A *fringing* or *shore reef* is a ridge of coral built up from the sea bottom so near the land that no navigable channel exists between it and the shore. Frequently breaks occur in the reef, and irregular channels and pools are created which are often inhabited by many different kinds of animals, some of them brilliantly colored.

A *barrier reef* is separated from the shore by a wide, deep channel. The Great Barrier Reef of Australia is over 1100 miles long and encloses a channel from 10–25 fathoms deep and in some places 30 miles wide. Often a barrier reef entirely surrounds an island.

An *atoll* is a more or less circular reef enclosing a lagoon. Several theories have been advanced to account for the production of atolls. Charles Darwin, who made extensive studies of coral reefs and islands, is responsible for the subsidence theory. According to Darwin, the reef was originally built up around an oceanic island which slowly sank beneath the ocean, leaving the coral reef enclosing a lagoon. John Murray believes that the island enclosed by the reef does not necessarily sink, but may be worn down by erosion.

Besides producing islands and reefs, corals play an important rôle in protecting the shore from being worn down by the waves. They have also built up thick strata of the earth's crust.

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## CHAPTER IV

### PHYLUM CTENOPHORA

The phylum CTENOPHORA (Gr. *ktenos*, of a comb; *phoreo*, I bear) includes a small group of free-swimming marine animals which are even more nearly transparent than the coelenterate jellyfishes. They have been placed by many authors under the phylum COELENTERATA, but the present tendency is to separate them

from that group and rank them as a distinct phylum. They are widely distributed, being especially abundant in warm seas.

Ctenophores are commonly called sea walnuts because of their shape (Fig. 143), or comb jellies on account of their jelly-like consistency and the comb-like locomotor organs arranged in eight rows on the sides of the body.

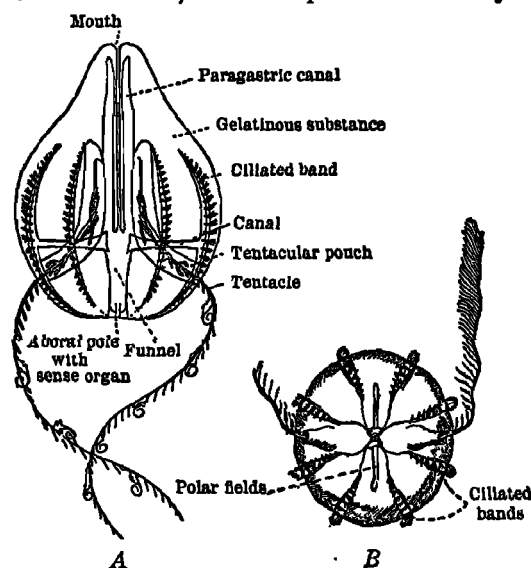


FIG. 143. — CTENOPHORA. TENTACULATA. A, *Hormiphora plumosa*. Side view. B, *Pleurobrachia pileus*. Aboral view. (A, after Chun; B, from Lankester's Treatise.)

A few species have a slender ribbon-like shape and may, like Venus' girdle (Fig. 146), reach a length of from six inches to four feet.

The general structure of a ctenophore is shown in figure 143. It is said to possess *biradial symmetry*, since the parts, though in general radially disposed, lie half on one side and half on the other side of a median longitudinal plane. An end view, as in figure 143, B, illustrates this fact. The mouth is situated at one end (oral) and a sense organ at the opposite or aboral end. Extending from near

the oral surface to near the aboral end are eight meridional ciliated bands; these are the locomotor organs. Each band has the cilia arranged upon it in transverse rows and fused at the base; each row thus resembles a comb. These are raised and lowered alternately, starting at the aboral end, and cause an appearance like a series of waves traveling from this point toward the mouth. The animal is propelled through the water with the oral end forward.

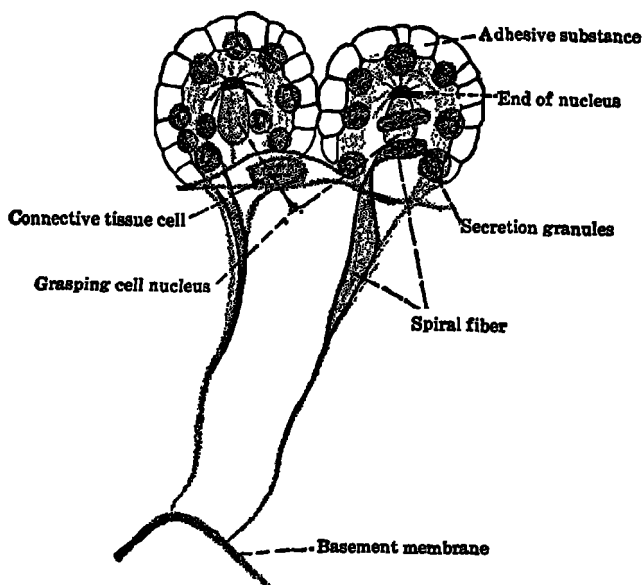


FIG. 144. — *Beroë ovata*. Mature adhesive cells or colloblasts. (After Schneider, from Dahlgren and Kepner.)

Light is refracted from these moving rows of cilia, and brilliant, changing colors are thus produced. Some species are phosphorescent.

Most ctenophores possess two solid, contractile tentacles (Fig. 143) which emerge from blind pouches, one on either side. With one exception, the tentacles are not provided with nematocysts as are those of the Cœlenterata, but are supplied with adhesive or glue cells called colloblasts (Fig. 144). The colloblasts produce a secretion of use in capturing small animals which serve as food. The spiral filament in each colloblast is contractile, and acts as a spring, often preventing the struggling prey from tearing the cell away.



The *mouth* (Fig. 143) opens into a flattened *stomodæum*, where most of the food is digested; this leads to the "*infundibulum*" or funnel which is flattened at right angles to the stomodæum. Six canals arise from the infundibulum. Two of these, called *excretory canals*, open to the exterior near an aboral sense organ; undigested food probably does not pass through them, but is ejected through the mouth. The two *paragastric canals* lie parallel to the stomo-

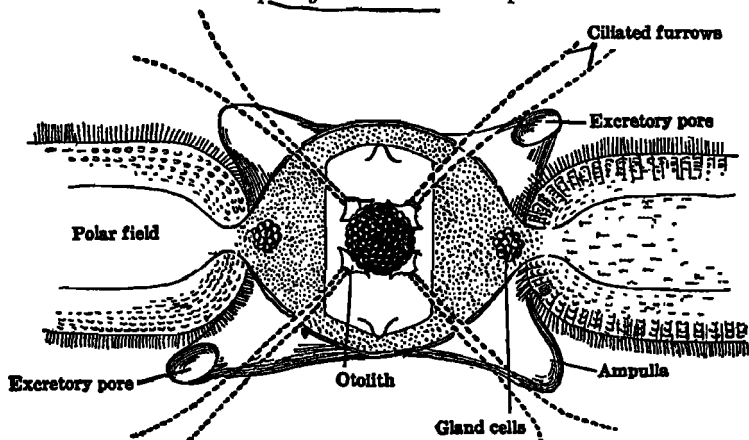


FIG. 145. — *Hormiphora plumosa*. Aboral sense organ viewed from above. (From Lankester's Treatise.)

dæum, ending blindly near the mouth. The two *tentacular canals* pass out toward the pouches of the tentacles, then each gives rise to four branches; these lead into *meridional canals* lying just beneath the ciliated bands.

The food of *Mnemiopsis* consists of plankton organisms. A particle of food that is caught in the current produced by the cilia in the auricular grooves is whirled about until it touches one of the small tentacles along the tentacular ridge. The tentacle, often with the aid of several other tentacles, entangles it and then contracts and it is drawn over the labial ridge into the labial trough toward the mouth. Thence the food passes through the mouth into the stomodæum. Undigested matter is cast out of the mouth or may enter the food canals and pass out through the anus.

The aboral sense organ (Fig. 145) is a *statocyst* or organ of equilibrium. It consists of a vesicle of fused cilia enclosing a ball of calcareous granules, the statolith, which is supported by four tufts of fused cilia. It is probable that when the body is at an angle, the

calcareous ball presses more heavily on the inclined side, and thus stimulates the ciliated bands on that side to greater activity. Just beneath the statocyst is a ciliated area supposed to be sensory in function, and on either side is a ciliated prolongation called the polar field.

Ctenophores are *hermaphroditic*. The *ova* are formed on one side and the *spermatozoa* on the other side of each meridional canal just beneath the ciliated bands (Fig. 143). The germ cells pass into the infundibulum and thence to the outside through the mouth. The fertilized eggs develop directly into the adult without the intervention of an asexual generation as in many coelenterates.

The *cellular layers* of ctenophores constitute a very small part of the body, most of it being composed of the transparent jelly-like *mesoglea*. The thin ciliated *ectoderm* covers the exterior and lines the stomodæum; and the *endoderm* also ciliated, lines the infundibulum and the canals to which it gives rise. The *muscle fibers* which lie just beneath the ectoderm and endoderm are derived from the *mesoderm* cells of the embryo. Ctenophores are, therefore, *triploblastic* animals, and represent a higher grade of development than that of the coelenterates.

**Classification.** — As noted above, ctenophores are triploblastic animals that exhibit radial combined with bilateral symmetry and possess eight radially arranged rows of paddle plates.

The CTENOPHORA differ from the coelenterates in several important respects besides the presence of a distinct mesoderm. With

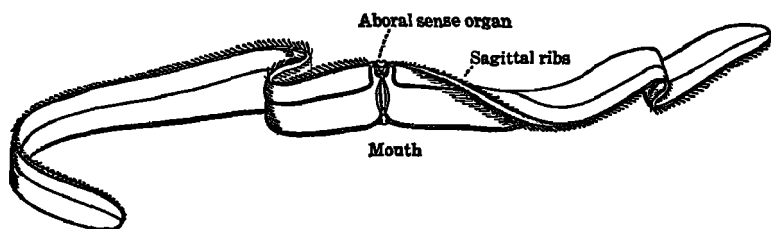


FIG. 146. — CESTIDA. *Cestus pectenalis*, Venus' girdle. (After Bigelow.)

one probable exception, ctenophores do not possess nematocysts, and the adhesive cells which take their place are not homologous to nematocysts. Their ciliated bands, aboral sense organs, and pronounced biradial symmetry are peculiarities which warrant placing ctenophores in a phylum by themselves. They probably evolved from coelenterate-like ancestors, but can no longer be

combined with that phylum. Two subclasses and four orders are listed here.

**SUBCLASS I. TENTACULATA.** — Two long aboral tentacles usually present.

**Order 1. CYDIPPIDA.** — Body spherical, ovoidal, or cylindrical; two long tentacles that may be retracted into aboral tentacular sacs.

*Pleurobrachia* (Fig. 143, B) is ovoidal and slightly compressed

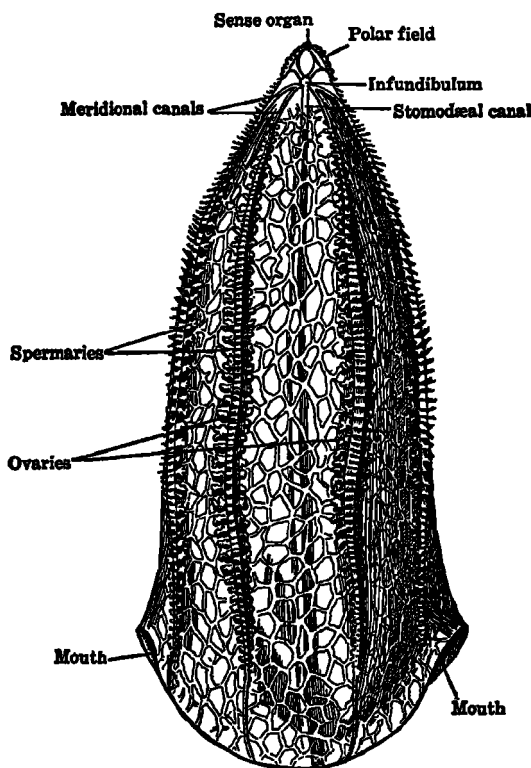


FIG. 147. — NUDA. *Beroë ovata*. (From Lankester's Treatise.)

laterally; the ciliated bands are eight in number and of equal length. *P. pileus* is about 2 cm. long and possesses tentacles about 15 cm. long; Long Island northward, Pacific coast, Europe.

**Order 2. LOBATA.** — Body ovate; two large oral lobes; tentacles and tentacular sacs in larva but not in adult.

*Mnemiopsis* has a pair of long projections (auricles) at the base of each oral lobe upon which the ciliated bands extend. *M.*

*leidyi* is about 10 cm. long; transparent and phosphorescent; Long Island to South Carolina.

**Order 3. CESTIDA.** — Body shaped like a ribbon; two tentacular sacs and two more or less rudimentary tentacles; many lateral tentacles.

*Cestus* is a genus containing several species. *C. veneris*, known as Venus' girdle (Fig. 146), may be two inches wide and nearly three

feet long; transparent but showing green, blue, and violet colors; tropical seas.

**SUBCLASS II. NUDA.** — Tentacles and oral lobes absent.

**Order 1. BEROIDEA.** — Body conical or ovate and laterally compressed; mouth very large and stomach voluminous; voracious.

*Beroë ovata* (Fig. 147) is about 10 cm. long; cosmopolitan.

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## CHAPTER V

### PHYLUM PLATYHELMINTHES

#### INTRODUCTION

The phylum PLATYHELMINTHES contains a group of animals which at first were included with other worm-like animals in a phylum called VERMES. They are known as flatworms because they are much flattened dorso-ventrally. Among them are both free-living and parasitic species; the former live principally in fresh or salt water; the latter are mostly endoparasitic. The parasitic flatworms are known as trematodes or flukes and cestodes or tapeworms. They are widely distributed among human beings and lower animals and are often pathogenic and sometimes bring about the death of the host. Free-living flatworms may be obtained from ponds and streams or in bodies of salt water. Each species has its own particular habitat which should be determined before collecting is attempted.

Four classes of PLATYHELMINTHES may be recognized; these are (1) TURBELLARIA, (2) TREMATODA, (3) CESTODA, and (4) NEMERTINEA. Most of the TURBELLARIA are free-living and inhabit either fresh or salt water; a few live in moist soil and a few are parasitic. The trematodes and cestodes are all parasitic and the nemertineans are free-living and mostly marine. The following are some of the classes and orders usually recognized.

**PHYLUM PLATYHELMINTHES.** — Unsegmented, triploblastic, bilaterally symmetrical animals; body flattened dorso-ventrally; no anus nor coelom present; usually hermaphroditic.

**CLASS I. TURBELLARIA.** — Mostly free-living; enteron present; body covered with cilia; usually rhabdites present; suckers usually absent.

**Order 1. ACCELA.** — Small marine species without an intestine. Ex. *Aphanostoma diversicolor*, *Polychærus caudatus*.

**Order 2. RHABDOCÆLIDA.** — Small fresh-water, marine, and terrestrial species; intestine simple, unbranched. Ex. *Stenostomum leucops*, *Microstomum lineare*, *Macrostomum appendiculatum*.

**Order 3. TRICLADIDA.** — Fresh-water, marine, and terrestrial species; intestine of three main trunks, each with many lateral diverticulæ. Ex. *Planaria maculata*, *Procotyla fluviatilis* (*Dendrocælum lacteum*), *Bdelloura candida*, *Bipalium kewensis*.

**Order 4. POLYCLADIDA.** — Marine species; central digestive cavity from which many diverticulæ arise.

**CLASS II. TREMATODA.** — Parasitic; enteron present; no cilia in adult, but cuticle present; suckers on ventral surface.

**SUBCLASS I. MONOGENEA.** — Principally ectoparasites; posterior organ of attachment with chitinous anchors and hooks; uterus usually containing one egg; development simple, direct. Parasites on fish, terrapin, and amphibians.

**SUBCLASS II. DIGENEA.** — Endoparasites; suckers without chitinous anchors and hooks; uterus long, containing many eggs; development by metamorphosis, with alternation of hosts. Parasites of invertebrates and vertebrates, including man.

**CLASS III. CESTODA.** — Endoparasites; enteron absent; no cilia in adult, but cuticle present; proglottids usually formed. Four orders to be described later.

**CLASS IV. NEMERTINEA.** — Mostly free-living, marine; alimentary canal with mouth and anus present; blood vascular system; long proboscis. Three orders to be described later.

## 1. CLASS I. TURBELLARIA

### (1) PLANARIA — A FRESH-WATER FLATWORM

**External features** (Fig. 148). — *Planaria maculata* belongs to the class TURBELLARIA and serves to illustrate the typical organ-

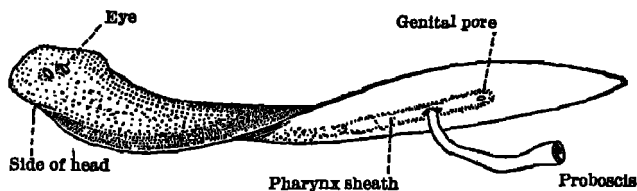


FIG. 148. — *Planaria polychroa*, a fresh-water turbellarian. (From Shipley and MacBride.)

ization of a platyhelminth better than any of the TREMATODA or CESTODA, since the latter are considerably modified for a parasitic existence. It is a flatworm found only in fresh water, usually cling-

ing to the underside of logs or stones. Like most of the members of the phylum PLATYHELMINTHES, its body is extremely flattened dorso-ventrally, and is bilaterally symmetrical. *Planaria* is broad and blunt at the anterior, and pointed at the posterior end. The length of an adult specimen may reach half an inch. The body contains so much coloring matter as to make the location of the internal structures difficult to determine in a living animal. In order to study *Planaria* successfully in the laboratory, the soft, contractile body is usually placed on a slide, and then pressed out slightly with a cover glass.

A pair of *eye spots* are present on the dorsal surface near the anterior end. The *mouth* is in a peculiar position near the middle of the ventral surface. From it the muscular *proboscis* may extend. Posterior to the mouth is a smaller opening, the *genital pore*. The surface of the body is covered with *cilia*, which propel the animal through the water. This is not the only method of locomotion, since muscular contraction is also effective.

**Morphology.** — A study of the structure of the adult and of the early embryonic stages shows *Planaria* to be a *triploblastic* animal possessing the three germ layers, ectoderm, mesoderm, and endoderm, from which several systems of organs have been derived. The mesoderm lying between the body wall and the intestine consists of large cells, the parenchyma or mesenchyme, with long, irregular processes among which are large intercellular spaces. There are well-developed muscular, nervous, digestive, excretory, and reproductive systems (Fig. 149); these are constructed in such a way as to function without the coordination of a circulatory system, respiratory system, coelom, and anus.

**Digestive system.** — The digestive system (Fig. 149) consists of a *mouth*, a *pharynx* lying in a muscular sheath, and an *intestine* of three main trunks with a large number of small lateral extensions. The muscular pharynx can be extended as a proboscis (Fig. 148); this facilitates the capture of food. Digestion is both *intercellular* and *intracellular*, i.e. part of the food is digested in the intestinal trunks by secretions from cells in their walls; whereas other food particles are engulfed by pseudopodia thrust out by cells lining the intestine, and are digested inside of the cells in vacuoles. The digested food is absorbed by the walls of the intestinal trunks, and, since branches from these penetrate all parts of the body, no circulatory system is necessary to carry nutriment

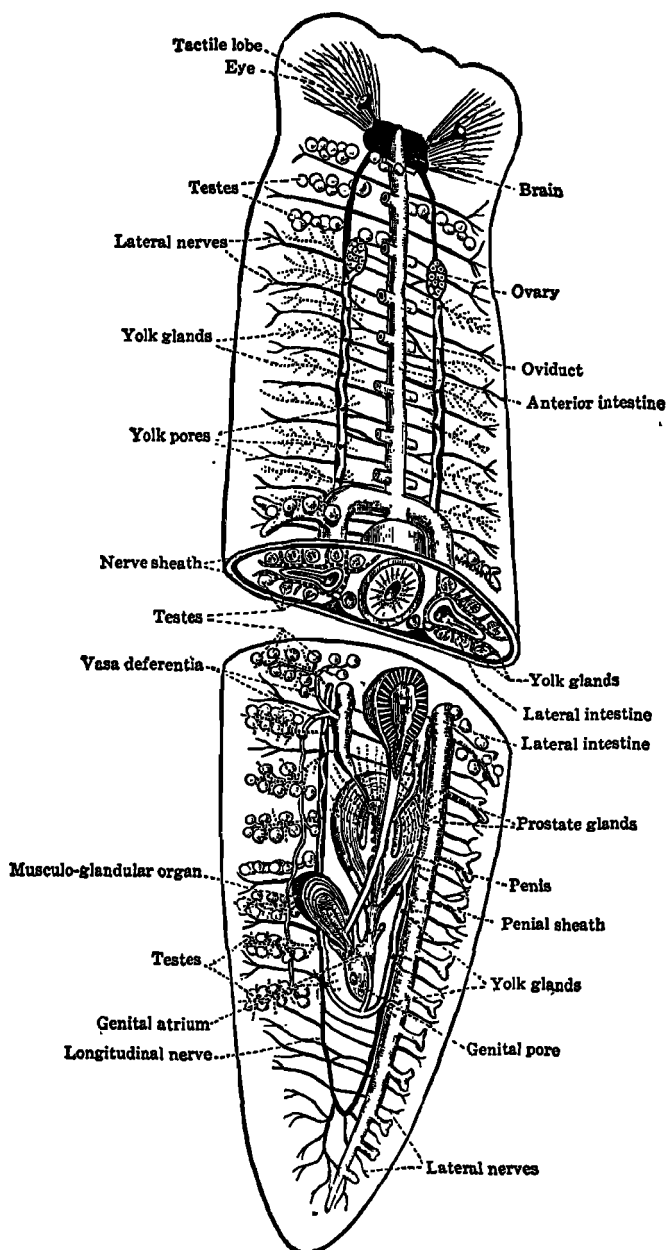


FIG. 149. — *Procoityla fluviatilis* (*Dendrocoelum lacteum*). Diagram showing the structure of a fresh-water turbellarian. (From Gamble.)



from one place to another. As in *Hydra*, no *anus* is present, the *feces* being ejected through the mouth.

The food of *Planaria* consists largely of small living crustaceans and worms and dead animals. These are captured by the proboscis

and ingested after being covered with slime secreted by the slime glands; or the pharynx is attached to the prey, digestive fluid is poured out and the dissolved particles are pumped into the intestine.

*Excretory system.* — The excretory system comprises a pair of longitudinal, much-coiled tubes, one on each side of the body; these are connected near the anterior end by a transverse tube, and open to the exterior by two small pores on the dorsal surface. The longitudinal and transverse trunks give off numerous finer tubes which ramify through all parts of the body, usually ending in a *flame cell* (Fig. 150). The flame cell is large and hollow, with a bunch of flickering cilia extending into the central cavity.

Since it communicates only with the excretory tubules it is considered excretory in function, though it may also carry on respiratory activities.

*Muscular system.* — The power of changing the shape of its body, which may be observed when *Planaria* moves from place to place, lies principally in three sets of muscles, a circular layer just beneath the ectoderm (Fig. 151), external and internal layers of longitudinal muscle fibers, and a set of oblique fibers lying in the mesoderm.

*Nervous system and sense organs.* — *Planaria* possesses a well-developed nervous system, consisting of a bilobed mass of tissue

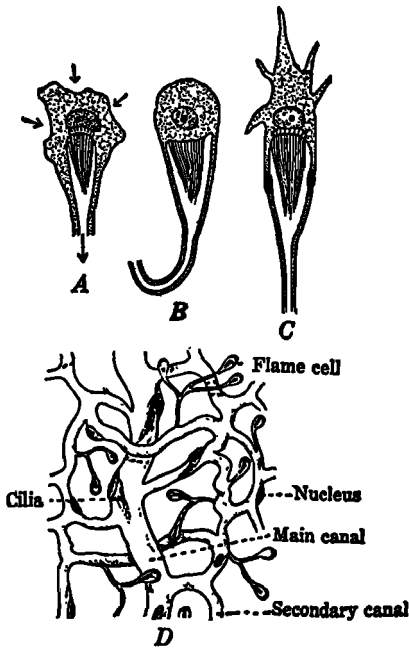


FIG. 150. — Flame cells and excretory ducts of PLATYHELMINTHES. A, from *Planaria*. B, from miracidium stage of liver fluke, *Fasciola*. C, from tapeworm, *Taenia*. D, excretory canals ending in flame cells. (A, B, C, after Kerr; D, after Benham.)

just beneath the eye spots, called the *brain* (Fig. 149) and two lateral *longitudinal nerve cords* connected by transverse nerves.

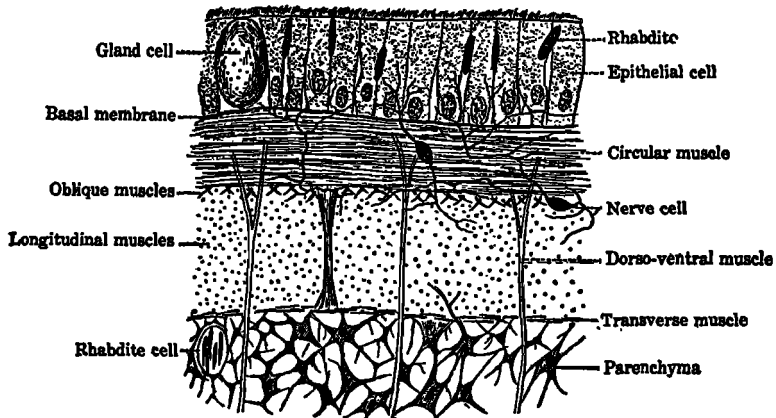


FIG. 151. — *Procotyla fluviatilis* (*Dendrocoelum lacteum*). Section through the skin. (After Hallez, from Petrunkevitch.)

From the brain, nerves pass to various parts of the anterior end of the body, imparting to this region a highly sensitive nature.

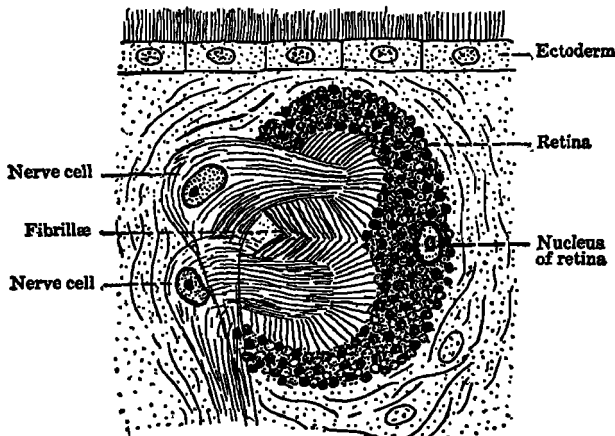


FIG. 152. — TURBELLARIA. *Planaria*. Histology of the eye. (After Hesse-Doflein, modified.)

Each eye (Fig. 152) consists of a highly pigmented retina of a single cup-shaped cell, inside of which are from two to thirty nerve cells, the fibrillæ of which are in contact with the retina and the opposite ends united into an optic nerve that passes to the

brain. There is no lens but the ectoderm over the eye is not pigmented. The ciliated pits on either side of the head contain special sensory cells with long cilia, and are connected with the underlying nervous network. In some TURBELLARIA tentacles occur near the anterior end with very long cilia; these are probably organs of chemical sense that aid in finding food. Cells, probably of chemical sense, are scattered over the surface of certain rhabdocœles. An otocyst located above the brain is present in some TURBELLARIA.

*Reproductive system.* — Reproduction is by *fission* or by the sexual method. Each individual possesses both male and female organs, *i.e.* is *hermaphroditic*. The *male organs* (Fig. 149) consist of numerous spherical *testes* connected by small tubes called *vasa deferentia*; the *vas deferens* from each side of the body joins the *cirrus* or *penis*, a muscular organ which enters the *genital cloaca*. A *seminal vesicle* lies at the base of the penis, also a number of unicellular *prostate glands*. Spermatozoa originate in the testes, and pass, by way of the *vasa deferentia*, into the seminal vesicle, where they remain until needed for fertilization. The *female reproductive organs* comprise two *ovaries*, two long *oviducts* with many yolk glands entering them, a *vagina*, which opens into the genital cloaca, and the *uterus*, which is also connected with this cavity. The *eggs* originate in the ovary, pass down the oviduct, collecting yolk from the yolk glands on the way, and finally reach the uterus. Here fertilization occurs, and *cocoons* are formed, each containing from four to more than twenty eggs, surrounded by several hundred yolk cells. During copulation spermatozoa from one animal are transferred by the penis to the other member of the pair. The genital organs are so constructed that self-fertilization is prevented and cross-fertilization assured.

*Regeneration and starvation.* — Planarians show remarkable powers of regeneration. If an individual is cut in two (Fig. 153), the anterior end will regenerate a new tail (*B*, *B'*), while the posterior part develops a new head (*C*, *C'*). A crosspiece (*D*) will regenerate both a head at the anterior end, and a new tail at the posterior end (*D'* — *D''*). The head alone of a Planarian will grow into an entire animal (*E* — *E''*). Pieces cut from various parts of the body will also regenerate completely. No difficulty is experienced in grafting pieces from one animal upon another, and many curious monsters have been produced in this way.

New tissue appears to be formed by the differentiation of formative cells, most of which migrate through the parenchyma to the region of differentiation. Dedifferentiation and redifferentiation do not seem to occur.

If *Planaria* is starved it absorbs its internal organs as food, in regular order; first the mature eggs are absorbed, then the yolk glands, the rest of the reproductive organs, parenchyma, intestine, and muscles. The size of the body decreases during this process; for example, in certain experiments the animals decreased from 13 mm. long and 2 mm. broad to 3.5 mm. long and 0.5 mm. broad in nine months. When starved specimens are given food, they regenerate the lost organs and become normal in size.

#### Axial gradients. —

*Planaria* is an animal that illustrates admirably the theory of axial gradients. The pri-

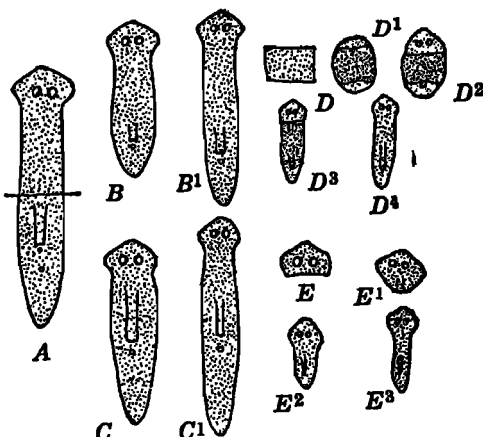


FIG. 153. — *Planaria*. Diagrams illustrating the regeneration of entire animals from small pieces. (From Morgan.)

mary axis or axis of polarity is an imaginary line extending from the anterior to the posterior end of the body. In *Planaria* the head has a relatively high rate of metabolism and dominates the rest of the body. Experiments have shown that a gradient of metabolic activity proceeds from the anterior to the posterior end. For example, if planarians are cut into four pieces the anterior piece will be found to use up more oxygen and give off more carbon dioxide than any of the others; the second piece comes next in its rate of metabolism; the third piece next; and the tail piece gives the lowest rate of all. Thus is demonstrated an axial gradient in the metabolism of the animal from the anterior to the posterior end. This is particularly well brought out in older planarians especially at the time of transverse division.

When a planarian is young, it is relatively short and its whole body, especially the head, has a relatively high rate of metabolism.

As it grows older it becomes longer and its whole metabolic rate slows down. When young, the high metabolic rate of the head was able to exercise a dominance, through the transmission of stimuli down the gradient, over the entire length of the animal. With a slowing down of the metabolic rate of the apical end and an increase in the length of the path over which the impulse travels, there comes a time when the apical end can no longer maintain a physiological dominance over the entire axis. At the point where dominance fades out, an independent part of the body arises through what is known as physiological isolation. The isolated piece, the second zooid, has its own gradient, the metabolic rate of the anterior end being the highest. This region now becomes a new apical end or, morphologically speaking, the head of a new zooid. No structural indications of a new individual are visible, however, at this time. The only tests of

the presence of a second or third individual are physiological tests. The isolated posterior zooid now forms a new head, with eyes, brain, and other parts. The new head then reorganizes the rest of the piece into a complete new individual.

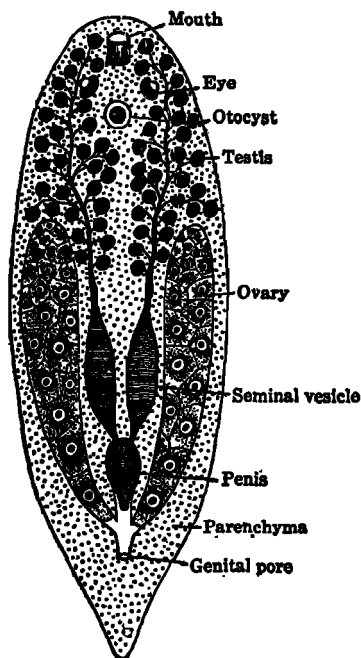


FIG. 154. — ACCELA: plan of structure. (From von Graff.)

## (2) OTHER TURBELLARIA

The four orders of TURBELLARIA may be distinguished by the presence or absence of an intestine and its character when present. The ACCELA have no intestine; in the RHABDOCCELIDA the intestine is a single straight tube; three main branches characterize the intestine in the TRICLADIDA; and many branches form a central cavity in the POLYCLADIDA. The principal features of the TURBELLARIA have been illustrated

in *Planaria*. The body is soft and usually less than an inch in length, more or less completely covered with cilia and with

slime secreted by glands in the integument or parenchyma. Rod-shaped bodies, called rhabdites, of unknown function are formed in special cells, among or beneath the ectoderm cells, and distributed to the ectoderm cells (Fig. 151). The parenchyma completely fills the space between the body wall and intestine, hence there is no coelom present. The digestive system includes a conspicuous muscular pharynx. Associated with the excretory system are the flame cells. Most species are hermaphroditic, and the reproductive organs are complex and arranged so as to prevent self-fertilization. The eggs are laid by many species in capsules attached to solid objects in the water, such as stones or vegetation. Fresh-water, marine, and a few terrestrial species occur. Most of them feed on other small animals but a few are parasitic.

**Order 1. ACCELA** (Fig. 154). — These have no muscular pharynx and are without an intestine, the latter being represented by a group of endoderm cells. The ACCELA are small and marine in habitat, and may be found among rocks and seaweed. One species, *Convoluta hensenii*, is a free-swimming plankton organism; another, *C. roscoffensis*, has symbiotic algæ living in its parenchyma.

**Order 2. RHABDOCCELIDA.** — The intestine in this order is a straight tube, sometimes with side pouches, and the mouth is located near the anterior end. About one half of the species are marine; the rest live in fresh water and a very few, on land. Some species, such as *Stenostomum leucops*, and *Microstomum lineare* consist of chains of individuals resulting from incompleting transverse division (Fig. 155). The last-named species possess nematocysts derived from ingested hydras (see page 24). Certain species, such as *Typhloplana viridata*, are usually colored green by symbiotic algæ. A

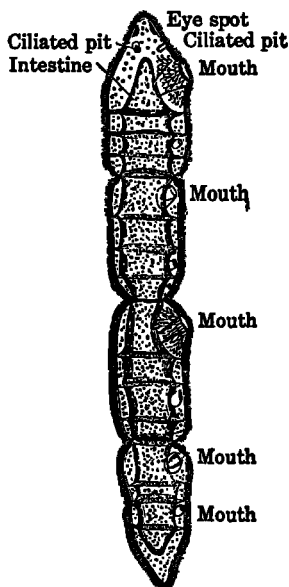


FIG. 155. — RHABDOCCELIDA. *Microstomum lineare*, undergoing division. The individual has first divided into two, near its middle, and each of these has again divided. Each of the four zooids has again divided into two, and so on, till sixteen individuals are here marked out. (From v. Graff.)

separate order, the ALLOIOCCELA, is sometimes employed to include species in which the intestine has side pouches.

**Order 3. TRICLADIDA.** — The intestine of the triclads consists of three main branches, each with many diverticulæ. The mouth

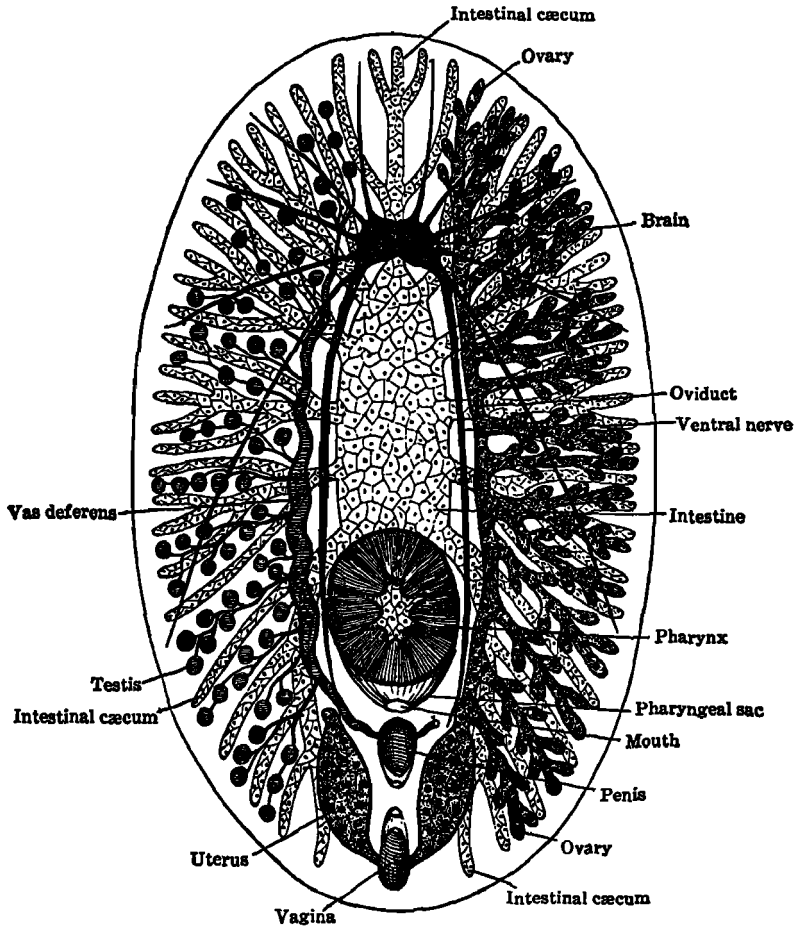


FIG. 156. — POLYCLADIDA: plan of structure, ventral view. (From von Graff.)

is near the center of the ventral surface. Three suborders are recognized.

**Suborder 1. PALUDICOLA.** — Fresh-water or brackish-water species, including *Planaria maculata* and about eight other American species of this genus. *Procotyla fluviatilis* (*Dendrocælum*).

*lacteum*) is a translucent species and its organs are easier to observe than those of *Planaria*; it has an adhesive disk on the anterior end. *Polycelis coronata* has many eyes arranged somewhat like a coronet, and *Phagocata gracilis* possesses many pharyngeal tubes lying in a common chamber and opening separately into the intestinal tract.

**Suborder 2. MARICOLA.** — Marine species, a few parasitic, with the mouth located in the posterior part of the body. This group includes *Procerodes whealandi*, and *Bdelloura candida*, which attaches itself to the living crab, *Limulus*. *Bdelloura* is of particular value for study because of the absence of pigment and, hence, its internal organs are clearly visible.

**Suborder 3. TERRICOLA.** — These so-called land planarians live in very moist places and resemble small slugs. *Bipalium kewensis* is a cosmopolitan species that is an inhabitant of the tropics but may appear in greenhouses in temperate regions on tropical plants; it may reach a length of one foot.

**Order 4. POLYCLADIDA** (Fig. 156). — This order contains marine species only; they have a central digestive cavity, from which branches extend to various parts of the body, and a posteriorly located mouth. Many polyclads are very broad and thin and may reach a length of six inches or more. *Planocera inquilina* lives in the mouth cavity of the gastropod *Fulgur*; *Stylochus ellipticus* is a common large species on the New England coast and possesses many frontal and marginal eye spots; *Leptoplana variabilis* has two groups of cerebral ocelli of about thirty each, and two groups of dorsal ocelli of about fifteen each.

## 2. CLASS II. TREMATODA

### (1) FASCIOLA HEPATICA — A LIVER-FLUKE

The liver-fluke is a flatworm which lives as an adult in the bile ducts of the liver of sheep, cows, pigs, etc., and is occasionally found in man. Figure 157 shows the shape and most of the anatomical features of a mature worm. The *mouth* is situated at the anterior end and lies in the middle of a muscular disk, the *anterior sucker*. A short distance back of the mouth is the *ventral sucker*; it serves as an organ of attachment. Between the mouth and the ventral sucker is the *genital opening* through which the eggs pass to the exterior. The *excretory pore* lies at the extreme



posterior end of the body, and another pore, the opening of Laurer's canal, is situated in the mid-dorsal line about one third the length of the body from the anterior end.

The *digestive system* is simple. The *mouth* opens into a short globular *pharynx* which leads into another short tube, the *oesophagus*. The *intestine* (Fig. 158) consists of two branches, one extending from near the anterior to the posterior end on each side of the body. Many small branches are given off from the intestine as in *Planaria* (Fig. 149) and no circulatory system is, therefore, necessary for the transportation of food material.

The *excretory system* is similar to that of *Planaria* (Fig. 150; p. 210), but only one main tube and one exterior opening are present. The *nervous system* also resembles that of *Planaria* (Fig. 149).

The *suckers* are provided with special sets of *muscles* enabling them to fasten the animal to its host. Three layers of muscles lie just beneath the ectoderm: (1) an outer circular layer, (2) a middle longitudinal layer, and (3) an inner diagonal layer.

The body of the liver-fluke is *triploblastic*. The *ectoderm* is a thin, hard covering often called the *cuticle*; it protects the underlying tissues from the juices of the host. The ectoderm contains chitinous scales and unicellular glands. The *endoderm* lines the alimentary tract. The *mesoderm* is represented by the muscles, the excretory organs, the reproductive ducts, and the parenchyma. The *parenchyma* is a loose tissue lying between the body wall and the alimentary canal; within it are embedded the various internal organs described above, as well as the reproductive system.

Both male and female *reproductive organs* are present in every adult (Fig. 157); they are extremely well developed, and, as in *Planaria*, quite complex. The *male organs* are as follows: (1) a pair of branched *testes* in which the spermatozoa arise; (2) two ducts, the *vasa deferentia*, which carry the spermatozoa from the testes to (3) a pear-shaped sac, the *seminal vesicle*; (4) a convoluted tube, the *ejaculatory duct*, which leads to the end of (5) a muscular copulatory organ, the *penis*.

The *female organs* are (1) a single-branched *ovary* (Fig. 157) in which the eggs are produced; (2) a convoluted *oviduct* which transports the eggs from the ovary to (3) the *shell gland*, at which place (4) the *vitelline* or *yolk duct* brings in and surrounds the eggs with yolk globules derived from (5) the *vitelline* or *yolk glands*

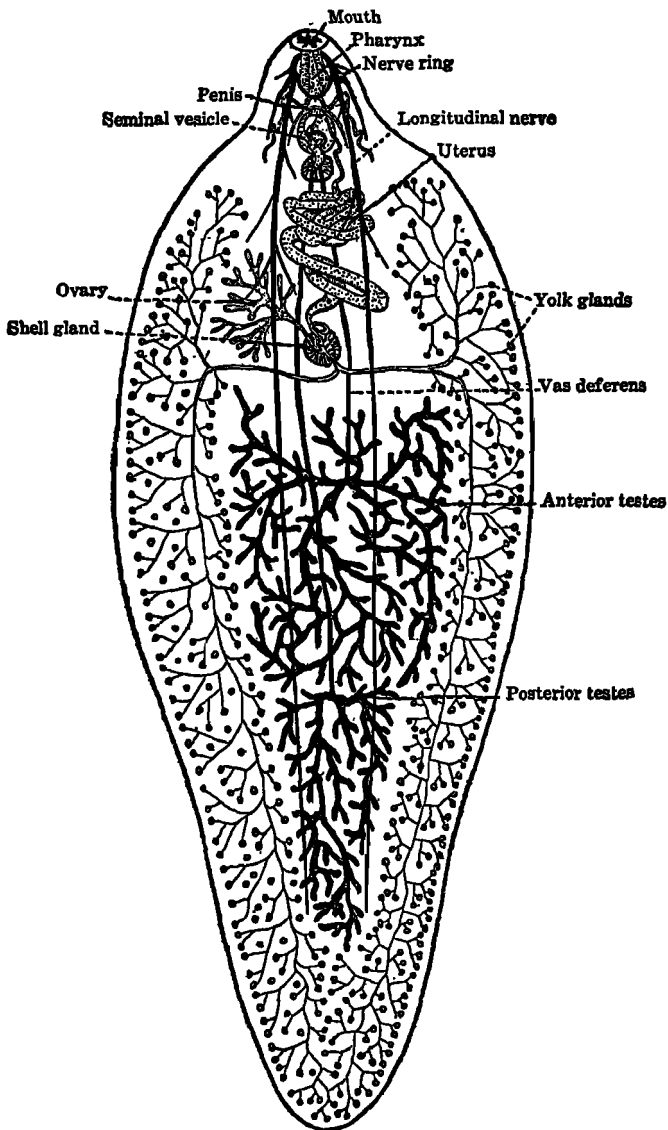


FIG. 157. — *Fasciola hepatica*. Diagram of the reproductive and nervous systems. (After Leuckart, modified.)

(Fig. 157); the shell gland then furnishes a chitinous shell, and the eggs pass on into (6) a tube called the *uterus*, which leads to the *genital pore*.

One liver-fluke may produce as many as five hundred thousand eggs, and, since the liver of a single sheep may contain more than two hundred adult flukes, there may be one hundred million eggs formed in one animal. The *eggs segment* in the uterus of the fluke (Fig. 158, A), then pass through the bile ducts of the sheep into its intestine, and finally are carried out of the sheep's body with the faeces. Those eggs that encounter water and are kept at a temperature of about 75° F. continue to develop, producing *ciliated larvæ* (B) which escape through one end of the egg-shell and swim about. Each larva, called a *miracidium*, possesses a double *eye spot* on the dorsal surface near the anterior end, a pair of *excretory organs*, the *nephridia*, and a number of centrally placed *germ cells*. It swims about until it encounters a certain fresh-water snail, *Lymnæa truncatula* of Europe, or probably *Lymnæa humilis* in this country. If no snail is found within eight hours, the larva dies.

When a snail is reached, the larva forces its anterior proboscis into its tissue, and by a whirling motion bores its way into the soft parts of the body. Here in about two weeks it changes into a sac-like *sporocyst* (Fig. 158, C). Each *germ cell* within the sporocyst, after passing through blastula and gastrula stages, develops into a second kind of larva, called a *redia* (D). The rediæ soon break through the wall of the sporocyst and enter the tissue of the snail. Here, by means of germ cells (D) within their bodies, they usually give rise to one or more generations of *daughter rediæ* (E), after which they produce a third kind of larva known as a *cercaria* (F). The cercariæ leave the body of the snail, swim about in the water for a time, and then encyst (G) on a leaf or blade of grass. If the leaf or grass is eaten by a sheep, the cercariæ escape from their cyst wall and make their way from the sheep's alimentary canal to the bile ducts, where they develop into mature flukes in about six weeks.

It will be seen from the above description that the life history of the liver-fluke is complicated by the interpolation of several generations which develop from unfertilized germ cells;

(1) The fertilized egg produces a ciliated larva, the miracidium (Fig. 158, B);

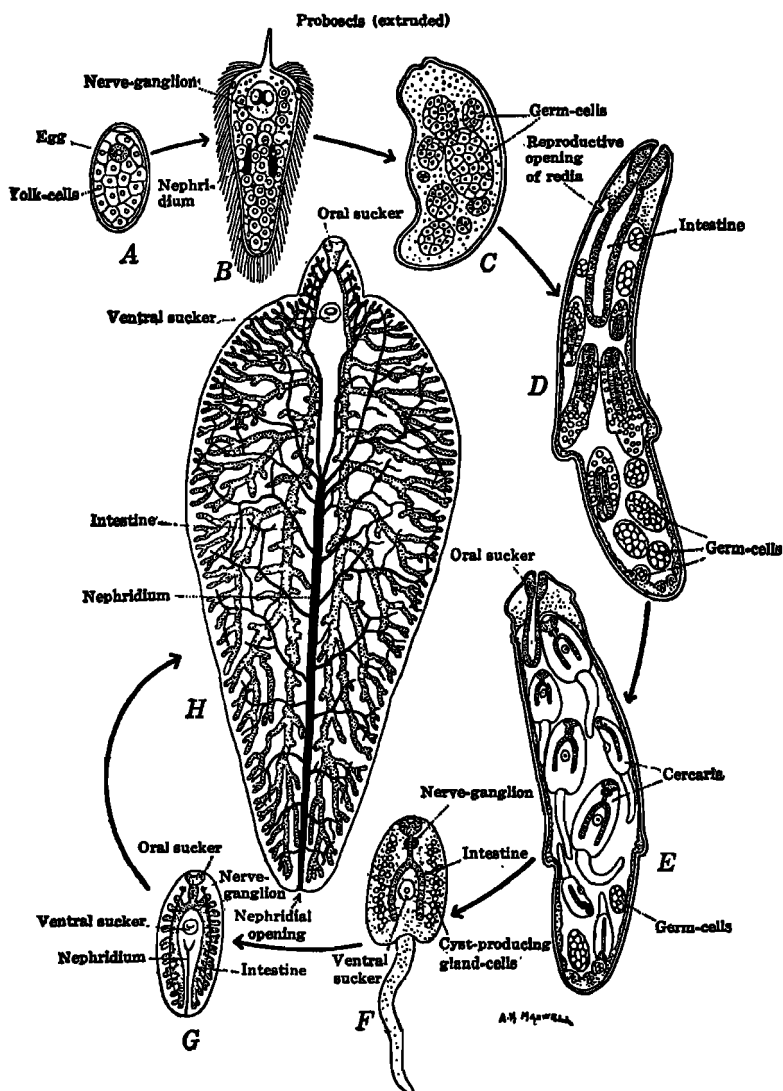


FIG. 158. — *Fasciola hepatica*; life-cycle. A, "egg." B, miracidium. C, sporocyst. D, E, rediae. F, cercaria. G, tail-less encysted stage. H, adult (neither reproductive organs nor nervous system are shown). (From Kerr.)

(2) The miracidium changes to a sporocyst (*C*) within which rediæ (*D*) are developed from unfertilized germ cells (*C*);

(3) The rediæ produce other rediæ (*E*) from unfertilized germ cells (*D*);

(4) The rediæ finally give rise to cercariæ (*F*) from unfertilized germ cells (*E*); and

(5) The cercariæ develop into mature flukes (Fig. 157).

The great number of eggs produced by a single fluke is necessary, because the majority of the larvæ do not find the particular kind of snail, and the cercariæ to which the successful larvæ give rise have little chance of being devoured by a sheep. The generations within the snail of course increase the number of larvæ which may develop from a single egg. This complicated *life history* should also be looked upon as enabling the fluke to gain access to new hosts. The liver-fluke is not so prevalent in the sheep of this country as in those of Europe.

## (2) OTHER TREMATODA

The trematodes resemble TURBELLARIA in many respects but differ from them in others, largely because of specialization for a parasitic existence. Organs of attachment and of reproduction are highly developed but organs of locomotion, sense, and digestion are reduced or lost entirely. Most trematodes are small ranging from 1 mm. to 2 or 3 cm. in length. Suckers are present on the ventral surface varying in size and location according to the species. The ectoderm cells of trematodes are sunk into the parenchyma and the body is covered with a non-cellular homogeneous cuticula often armed with spines. Beneath the cuticula is a dermo-muscular sac consisting of an outer layer of circular muscles, a thinner middle layer of diagonal muscles, and an inner layer of longitudinal muscles. There are also dorso-ventral muscles and muscles connected with the suckers. No cœlom is present, the body between the intestine and dermo-muscular sac being filled with parenchyma.

The digestive system consists of a mouth located in the oral sucker, a muscular pharynx, and a thin cesophagus into which salivary glands pour their secretions; then comes an intestine of two branches more or less elongated and ending blindly. The food of trematodes consists of the intestinal contents of the host, mucus, and other secretions, epithelial cells, etc., according to the species. Undigested particles are egested through the mouth. Excretory

matter is collected by the flame cells (Fig. 150) from the surrounding parenchyma, passes through capillaries into collecting tubes, and is carried to a bladder, usually near the posterior end, and then expelled through an excretory pore. There are no circulatory nor respiratory systems. The nervous system resembles that of the TURBELLARIA. There are two cerebral ganglia above the pharynx, connected by a commissure; from these ganglia three pairs of nerve cords arise and pass backward, being located near

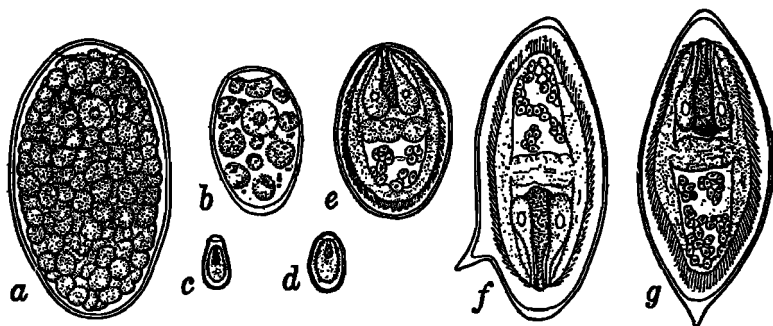


FIG. 159. — TREMATODA. Eggs of certain species that live in man. (After Cort.) a, *Fasciolopsis buski*, an intestinal fluke; China. b, *Paragonimus westermani*, a lung fluke; Far East, America. c, *Clonorchis sinensis*, a liver fluke; Far East. d, *Metagonimus yokogawai*, an intestinal fluke; China, Japan. e, *Schistosoma japonicum*, a blood fluke; China, Japan, Philippines. f, *Schistosoma mansoni*, a blood fluke; Africa, America. g, *Schistosoma hæmatobium*, a blood fluke; Africa, Near East.

the dorsal, ventral, and lateral surfaces respectively. Adult trematodes have no sense organs.

The reproductive organs of trematodes are complex and life cycles usually involve several different hosts, which results in enormously increased powers of reproduction. The production of large numbers of offspring is necessary in parasitic animals since the chances that any one individual will reach a new host are rather slight. Most trematodes are hermaphroditic. The description and illustration of the reproductive organs of the liver-fluke (p. 218) indicate their character. The eggs (Fig. 159) of one worm are supposed to be fertilized usually by spermatozoa from the same worm, although cross-fertilization may occur. The larvæ that hatch from the eggs of ectoparasitic trematodes are ciliated and swim about until they attach themselves to a new host. Endoparasitic trematodes usually pass through a complicated life cycle as in the liver-fluke (Fig. 158).

A life cycle recently described, that of *Alaria mustelæ*, involves four different species of hosts. The sporocysts in (1) the snail, *Planorbula armigera*, produce cercariæ which penetrate into (2) tadpoles or frogs in which they become agamodistoma; these when eaten by (3) a mammal, such as a mink, raccoon, or mouse, become metacercariæ in the muscles or lungs; the metacercariæ grow to the adult state when eaten by (4) another mammal, such as a mink, weasel, cat, dog, or ferret, in the intestines of which they deposit their eggs. From the latter, miracidia hatch, which are capable of infecting the snail.

Many larval trematodes, the cercariæ, have been described, the adult stages of which are unknown. These cercariæ possess certain adult characteristics such as suckers, digestive and ex-

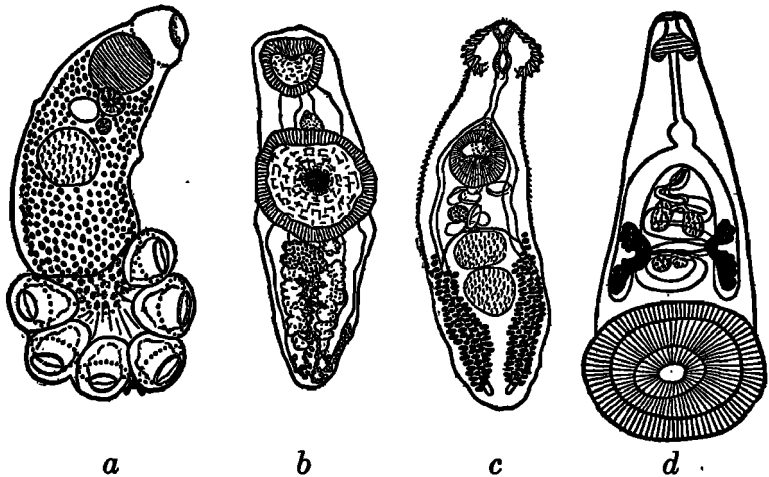


FIG. 160. — Types of adult trematodes. a, *Polystoma megacotyle*, from the mouth cavity of the turtle. b, *Gorgoderia minima*, from the bladder of the frog. c, *Stephanoprora gilberti*, from the intestine of aquatic birds. d, *Diplodiscus temperatus*, from the rectum of the frog. (a, after Stunkard; b, after Cort; c, after Ward; d, after Cary.)

cretory systems, and temporary larval characteristics, such as tails, stylets, and cystogenous and cephalic glands. Cercariæ may be obtained by placing fresh-water snails in a glass of water and watching for them with a hand lens as they emerge from these hosts. They have been given names and classified in various ways but their true relations can only be determined when the adults into which they develop become known.

**SUBCLASS MONOGENEA.** — The two subclasses of trematodes may be divided into seven orders, two in the subclass MONOGENEA and five in the subclass DIGENEA. The MONOGENEA are principally ectoparasites of fish, turtles, and amphibians. Each species is usually restricted to a single species of host. They attach themselves to the gills of fish but some species live in the mouth, cloaca, or bladder.

**Order 1. MONOPISTHOCOTYLEA.** — The members of this order have double excretory pores that are anterior and dorsal. The posterior organ is single; the vagina is unpaired; the uterus contains a single egg; and there is no genito-intestinal canal. A common genus is *Ancyrocephalus*, species of which occur on the gills of many fresh-water fish.

**Order 2. POLYPISTHOCOTYLEA.** — These possess multiple posterior organs, a double vagina, and a genito-intestinal canal. A genus that contains a number of species from North America is *Polystoma* (Fig. 160, a). It has six suckers in a circle or in two rows at the posterior end. Species have been described from the mouth cavity and urinary bladder of several species of turtles.

**SUBCLASS DIGENEA.** — This subclass contains endoparasitic trematodes including all of the species parasitic in man. Their life cycle involves two or more species of hosts. Two orders and five suborders may be recognized.

**Order 1. GASTEROSTOMATA.** — Trematodes with a single sucker at the anterior end and with the mouth in the center of the ventral surface; intestine, sac-like; genital pore at posterior end. These forms live in the intestine of both fresh-water and marine fish as adults and in bivalve mollusks as larvæ. *Bucepalus gracilescens* lives in marine fish and as a larva in the internal organs of the oyster.

**Order 2. PROSOSTOMATA.** — In this order the mouth is anterior and usually surrounded by a sucker, and a second sucker may be present on the ventral surface behind the anterior sucker or at the posterior end. All human trematodes belong here. Three suborders may be recognized:

(1) The **ASPIDOCOTYLEA** have a powerful ventral sucking organ or a series of small suckers, and are parasites of mollusks and cold-blooded vertebrates, such as *Aspidogaster conchicola* in bivalves.

(2) The **MONOSTOMATA** have an oral sucker but no ventral organ of attachment, and are parasitic mostly in birds and reptiles but not in man; an example is *Collyriclum faba* in the English sparrow.



(3) The HOLOSTOMATA have a special adhesive organ behind the acetabulum, a body with distinct anterior and posterior divisions and are parasitic in frogs, birds, and carnivorous mammals;

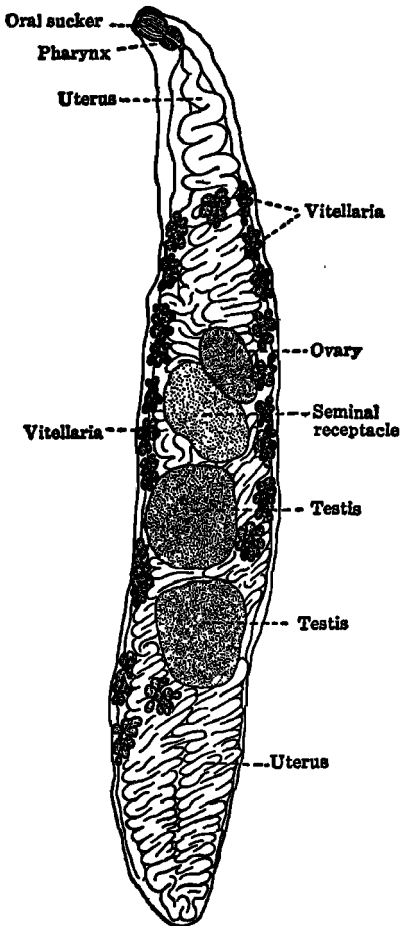


FIG. 161. — *Pneumonaces medioplexus*, a lung fluke from the frog. (After Cort.)

*Alaria arisæmoides* which lives in the red fox is an example.

(4) The AMPHISTOMATA (Fig. 160, *d*) are often conical, have a highly developed acetabulum that is terminal or sub-terminal and posterior to the reproductive organs, and are parasitic in amphibians, reptiles, birds, ruminants, and rodents; examples are *Diplo-discus temperatus* in the rectum of frogs and *Gastrodiscoides hominis* in man.

(5) The DISTOMATA have only oral and ventral suckers for purposes of attachment, and reproductive organs mostly or completely posterior to the ventral sucker; and the class includes hundreds of species parasitic in mammals and other vertebrates. All but two species of human trematodes belong to this suborder.

*Pneumonæces*, a genus that lives in the lungs of frogs and toads, is favorable material for laboratory study. The life history of *P. medioplexus* (Fig. 161) has been worked out experimentally in the laboratory

using *Rana pipiens* for the definitive host. It lives as an adult parasite in the lungs of the leopard frog and has larval stages in a snail, *Planorbula armigera*, and certain dragonflies of the genus *Sympetrum*. The parasites produce eggs in great numbers which pass from the lungs through the glottis into

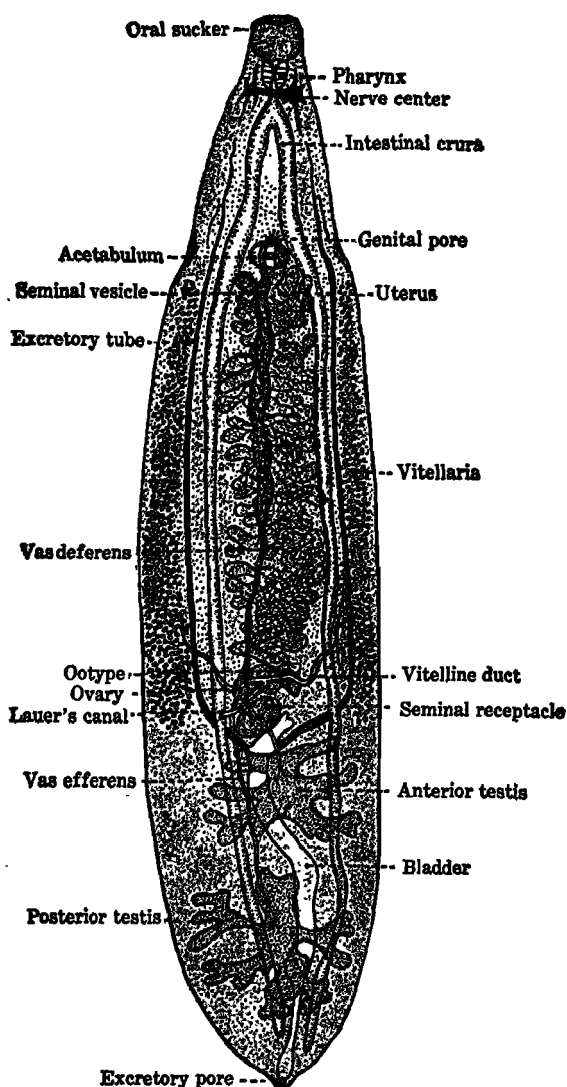


FIG. 162. — *Clonorchis sinensis*, a liver fluke that lives in man. (After Faust.)

the mouth cavity. They are swallowed, pass through the digestive tract and are voided with the faeces. The eggs, containing mature miracidia, are deposited in this way in the shallow water along the margins of ponds and lakes where snails are usually abundant. The miracidia remain alive within the eggs for weeks without hatching, and it is necessary for the snails to eat the eggs in order to become infected. The miracidia are small (25 microns in length) covered with a dense coating of long cilia, and move relatively slowly. The elongated, sausage-shaped daughter sporocysts are located in the digestive gland

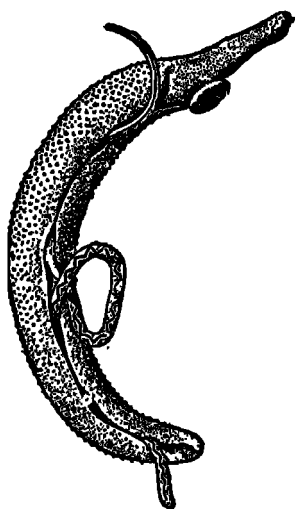


FIG. 163. — *Schistosoma haematobium*, a human blood fluke. The larger male is carrying the more slender female in the gynæcophoric canal. (From Augustine, after Manson-Bahr.)

of the snail where they give rise to comparatively few cercariæ which make their escape from the snail. Cercariæ swimming in the vicinity of a dragon-fly nymph are caught by the respiratory currents produced by the gills in the rectum, and are swept into the chamber of the branchial basket through the anal opening. They penetrate through the chitin into the tissues of the lamellæ, and the metacercariæ encyst shortly within thin, structureless, transparent, pliable cysts where they ordinarily attain maximum size in from fourteen to twenty days. The encysted metacercariæ remain in the lamellæ until the nymph transforms into an adult dragon-fly. Hundreds may be found in a single insect. They live here in a more or less inactive condition until the host dies in the fall of the year or until such a

parasitized dragon-fly is eaten by a leopard frog or a common toad. In the stomach of either animal the insect is sufficiently digested to free the metacercariæ. These are stimulated to activity by the digestive fluid and creep up the œsophagus in measuring-worm fashion. From the œsophagus they pass through the glottis into the lungs, where they reach maturity, under optimum conditions, in twenty-eight or thirty days from the time they enter the frog. The flukes grow considerably after attaining maturity. (Krull.)

It is impossible in the space available to describe in detail the morphology, and life cycles of the trematodes or to discuss their importance as pathogenic parasites of man and domesticated and other lower animals. The life histories of a few digenetic trematodes and a few facts about some of the important human species are presented in the accompanying tables.

THE LIFE HISTORIES OF A FEW DIGENETIC TREMATODES

SPECIES	FINAL HOST	HOST LARVA ENTERS AND CERCARLE FORMED	HOST CERCARLE ENTER: EATEN BY FINAL HOST
1. <i>Distomum atriventre</i>	Frogs and toads of North America	<i>Physa heterostrophia</i> , a snail	Not known
2. <i>D. retusum</i>	The frog, <i>Rana</i>	The snail, <i>Lymnaea stagnalis</i>	The snail, <i>Lymnaea stagnalis</i> , and larvae of caddice flies
3. <i>Gasterostomum fimbriatum</i>	Perch and pike, <i>Perca</i> and <i>Esox</i>	Fresh-water clams, <i>Unio</i> and <i>Anodonta</i>	<i>Leuciscus erythrophthalmus</i> , a small fish
4. <i>Monostromum flavum</i>	<i>Anas</i> , a duck	A snail, <i>Planorbis corneus</i>	Omitted
5. <i>Diplodiscus subclavatus</i>	Frogs, toads, and salamanders, <i>Rana</i> , <i>Bufo</i> , and <i>Triton</i>	Snails, <i>Planorbis</i> and <i>Cyclas</i>	Insect larvae frogs ( <i>Rana</i> ) and toads ( <i>Bufo</i> ). Often omitted

SOME COMMON TREMATODES OF MAN

	SCIENTIFIC NAME	DEVELOPMENTAL STAGES	GEOGRAPHICAL DISTRIBUTION	HOSTS
INTESTINAL FLUKES	<i>Fasciolopsis buski</i>	In water-grown vegetables	China, Indo-China, Formosa, Sumatra, India	Man (China); frequent in pigs (Formosa)
	<i>Heterophyes heterophyes</i>	In fresh-water fish	Egypt, China, Japan	Man, cat, dog, and fox in Egypt
	<i>Metagonimus yokogawai</i>	In trout	Korea, China, Japan	Man, cat, and dog

SOME COMMON TREMATODES OF MAN — *Continued*

	SCIENTIFIC NAME	DEVELOPMENTAL STAGES	GEOGRAPHICAL DISTRIBUTION	HOSTS
LIVER FLUKES	<i>Clonorchis sinensis</i> (Fig. 162)	In fresh-water fish	China, Japan, Korea, French Indo-China	Man, cat, dog, and fish-eating mammals
	<i>Fascioloides magna</i>	Not known; probably on vegetation	North America, along coast of Gulf of Mexico	Man
	<i>Opisthorchis filineus</i>	In fresh-water fish	East Prussia, Serbia, Annam, Philippines	Man, cat, dog
LUNG FLUKES	<i>Paragonimus westermani</i>	In fresh-water crabs	Japan, Korea, Formosa, Philippines, America	Man, tiger, dog, cat, pig
BLOOD FLUKES	<i>Schistosoma hæmato-bium</i> (Fig. 163)	In snails	Africa, Near East, Portugal, Australia	Man, monkey; experimentally in rat, mouse, monkey
	<i>Schistosoma mansoni</i>	In snails	Africa, West Indies, North and South America	Man
	<i>Schistosoma japonicum</i>	In snails	Japan, China, Philippines	Man, cat, dog, pig, etc.

## 3. CLASS III. CESTODA

## (1) TÆNIA — A TAPEWORM

The tapeworm, *Tænia solium*, is a common parasite which lives as an adult in the alimentary canal of man. A nearly related species, *T. saginata*, is also a parasite of man. *Tænia*, as shown in figure 164, is a long flatworm consisting of a knob-like head, the *scolex*, and a great number of similar parts, the *proglottids*, arranged in a linear series. The animal clings to the wall of the alimentary canal by means of *hooks* and *suckers* on the *scolex*. Behind the *scolex* is a short *neck* followed by a string of *proglottids* which gradually increase in size from the anterior to the posterior end. The worm may reach a length of ten feet and contain eight or nine hundred *proglottids*. Since the *proglottids* are budded off from the neck, those at the posterior end are the oldest. The production of *proglottids* may be compared to the formation of

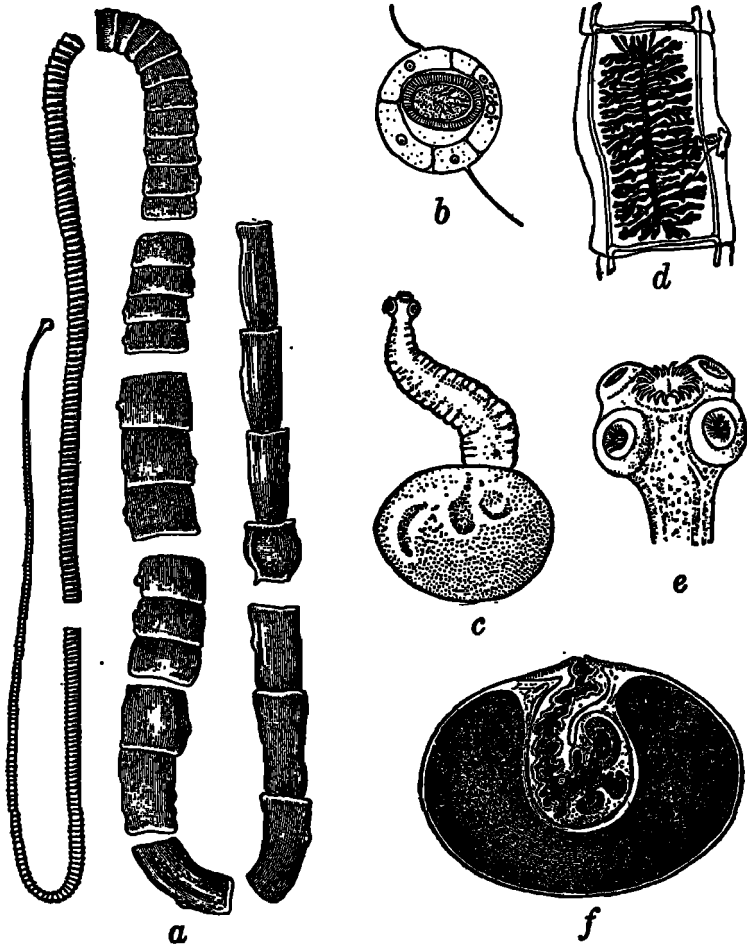


FIG. 164. — CESTODA, tapeworms living in man. a, *Tænia saginata*, adult; the beef tapeworm. b, *Tænia saginata*; egg surrounded by its membrane; note hooks within the egg. c, Cysticercus or bladderworm with head evaginated and capable of attachment to the intestinal wall. d, *Tænia saginata*, mature proglottid. e, *Tænia solium*, scolex showing hooks and suckers. f, Cysticercus, in median section showing scolex at bottom of invagination. (After various authors.)

ephyrae by the hydra-tuba of *Aurelia* (Fig. 128, *E*, *F*), and is called *strobilization*.

The *anatomy* of the tapeworm is adapted to its parasitic habits (Fig. 165). There is *no alimentary canal*, the digested food of the host being absorbed through the body wall. The *nervous system* is similar to that of *Planaria* and the liver-fluke, but not so well developed. Longitudinal *excretory tubes*, with branches ending

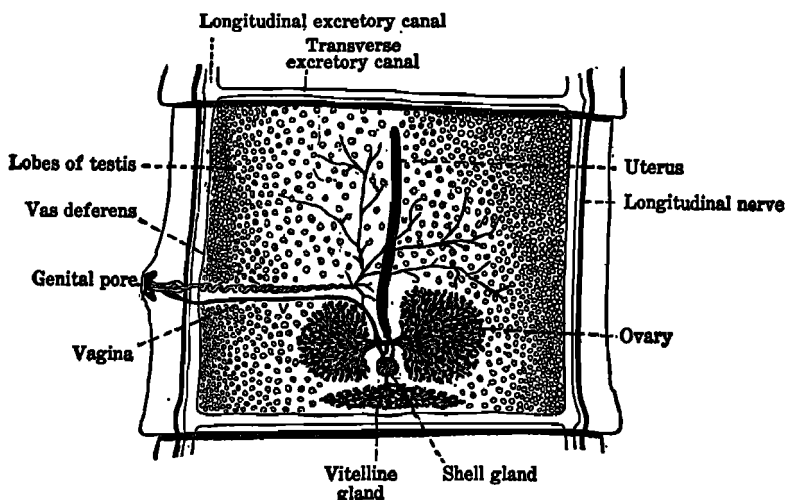


FIG. 165. — *Taenia saginata*. Mature proglottid of the "beef tapeworm" of man. (After Leuckart.)

in *flame cells*, open at the posterior end and carry waste matter out of the body.

A *mature proglottid* is almost completely filled with *reproductive organs*; these are shown in figure 165. *Spermatozoa* originate in the spherical *testes*, which are scattered about through the proglottid; they are collected by fine tubes and carried to the *genital pore* by way of the *vas deferens*. *Eggs* arise in the bilobed *ovary* and pass into a tube, the *oviduct*. Yolk from the *yolk gland* enters the oviduct and surrounds the eggs. A chitinous shell is then provided by the *shell gland* and the eggs pass into the *uterus*. The eggs have in the meantime been *fertilized* by spermatozoa, which probably come from the same proglottid, and move down the *vagina*. As the proglottids grow older the uterus becomes distended with eggs and sends off branches, while the rest of the reproductive

organs are absorbed. The ripe proglottids break off and pass out of the host with the faeces.

The eggs of *Tænia* develop into six-hooked embryos (Fig. 164, *b*) while still within the proglottid. If they are then eaten by a pig, they escape from their envelopes (Fig. 164, *c*) and bore their way through the walls of the alimentary canal into the voluntary muscles, where they form *cysts* (Fig. 164, *f*). A head is developed from the cyst wall and then becomes everted. The larva is known as a *bladder-worm* or *cysticercus* (Fig. 164, *c*) at this stage. If insufficiently cooked pork containing cysticerci is eaten by man, the bladder is thrown off, the head becomes fastened to the wall of the intestine, and a series of proglottids is developed.

## (2) OTHER CESTODA

The CESTODA or tapeworms are highly modified for a parasitic existence. They are all endoparasitic and almost all of them live as adults in the digestive tract of vertebrates and as larvæ in the tissues of vertebrates and invertebrates. No digestive system is present even in the simple trematode-like cestodes, and nutriment is absorbed through the surface of the body. Most cestodes are shaped like a band or ribbon (Fig. 164) and consist of many segments called proglottids (Fig. 165); these, however, are not true segments like those of higher invertebrates, such as the annelids. The adults are often several yards in length and consist of a small head or scolex, a short neck, and a long chain of proglottids or strobila. The scolex usually bears suckers, or acetabula, and is sometimes armed with hooklets. The neck is the growing region, from the posterior end of which proglottids are budded off. The proglottids increase in size as they are pushed back and various systems of organs develop in them.

Each proglottid usually possesses a genital pore on one of the lateral borders or on the surface, but some species have a separate uterine pore. The body is covered with a cuticula as in the trematodes and the internal organs lie in a mass of parenchyma cells in which are also embedded calcareous corpuscles. Circular, longitudinal, transverse, and dorso-ventral muscle fibers are present as in the trematodes and also nerve bundles in the scolex from which arise longitudinal nerve fibers. The excretory system likewise resembles that of the trematodes.

Tapeworms are hermaphroditic. The reproductive organs vary



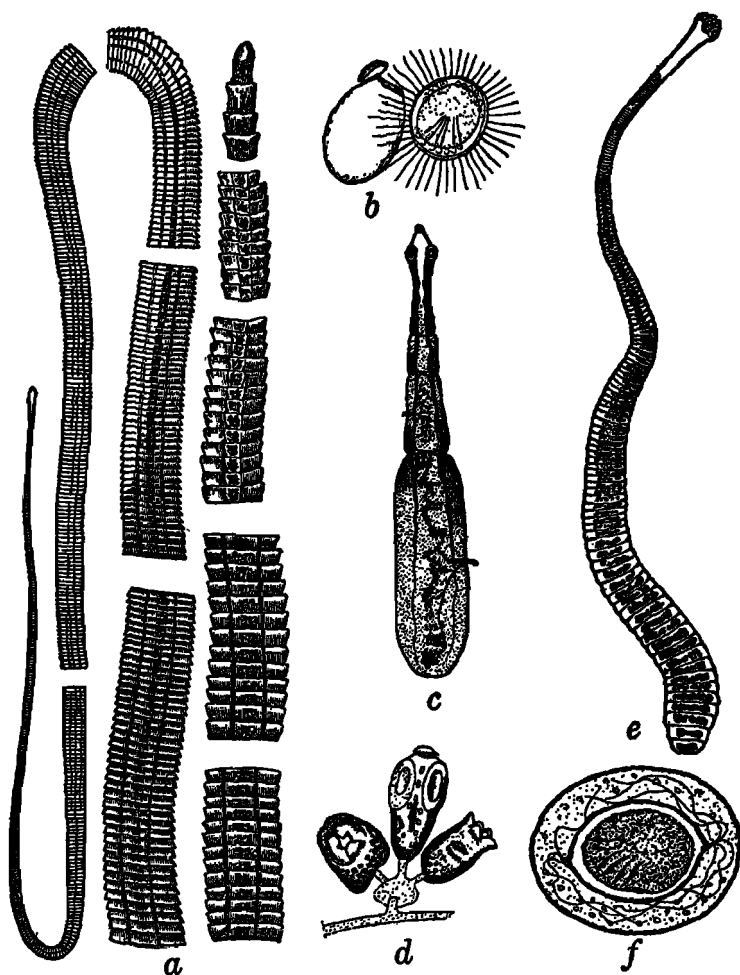


FIG. 166. — Cestodes that live in man. a, *Diphyllbothrium latum*, the fish tapeworm of man. b, *D. latum*; ciliated embryo (coracidium) escaping from egg. c, *Echinococcus granulosus*; adult stage that lives in the dog. d, *E. granulosus*; formation of scolices from the germinative membrane of a hydatid cyst. e, *Hymenolepis nana*, the dwarf tapeworm of man. f, *H. nana*, egg. (Mostly after Leuckart.)

in different groups; those of *Tænia*, already described (p. 232), indicate their character. Each proglottid contains a complete set of both male and female organs. Apparently the eggs formed in a proglottid are fertilized by spermatozoa from the same proglottid, although copulation is known to occur between proglottids of the same worm and of different worms. In some species the eggs are continually being discharged through a uterine pore, but in most species they are stored up in the proglottids which become "gravid," separate from the chain and pass out in the fæces of the host. The eggs in these proglottids contain embryos which, when fully developed, are called onchospheres; these are able to continue their development only when ingested by a proper host. The onchospheres escape from the egg and burrow through the intestinal wall into the body cavity or vascular spaces or into certain tissues. The onchospheres of the lower cestodes become spindle-shaped, hooked proceroids, which develop in a second intermediate host into worm-like, hookless plerocercoids. The larvæ of certain higher cestodes are called cysticeroids; they have a rudimentary bladder and may possess a tail. The true bladder-worms are (1) the small cysticercus which gives rise to one scolex, (2) the large cœnurus from which many scolices arise, and (3) the echinococcus or hydatid, which gives rise to daughter and grand-daughter cysts in which many scolices are developed from brood pouches (Fig. 166, *c*, *d*). The bladder-worms are the stage infective to the definitive host and each scolex may give rise to a tapeworm. Tapeworms, when alive, successfully resist the digestive juices of the host, but soon disintegrate when dead. They may live for many years; several cases are on record of tapeworms that lived for twenty years or more.

Four orders of cestodes will be mentioned here. Sometimes a subclass, CESTODARIA, is recognized in which is placed *Archigetes sieboldii*, a parasite in the cœlom of the annelid *Tubifex* which is not divided into segments and possesses only one set of reproductive organs, and several other similar species.

**Order 1. PSEUDOPHYLLIDEA.** — The tapeworms in this order have a scolex which is hollowed out on two opposite sides to form groove-like suckers or rarely have a single terminal sucker. The uterus is a sac-like cavity or consists of rosette-shaped coils. A uterine pore opens on the surface. The eggs are operculated, and the embryos are ciliated. The adults occur in reptiles, birds, and mammals.

The most important human species is the broad or fish tapeworm, *Diphyllobothrium latum* (Fig. 166, a), which has two intermediate hosts, fresh-water copepods and fish. Digestive disturbances, nervous symptoms, and anæmia may result from the infection.

SOME COMMON CESTODES OF MAN

SCIENTIFIC NAME	DEVELOPMENTAL STAGES	GEOGRAPHICAL DISTRIBUTION	Hosts
<i>Diphyllobothrium latum</i>	In copepods and fresh-water fish	World-wide, especially Europe, Africa, North America, Japan	Man, dog, cat, fox (Intestine)
<i>Echinococcus granulosus</i>	In liver, brain, lungs, etc., of man, pig, sheep, etc.	World-wide, especially Iceland, Australia, Argentine	Dog and other carnivores (Intestine)
<i>Hymenolepis nana</i>	Man, rat, mouse	World-wide	Man, rat, mouse
<i>Tænia saginata</i>	In muscles of cattle	World-wide	Man
<i>Tænia solium</i>	In muscles of pig	World-wide	Man

**Order 2. CYCLOPHYLLIDEA.** — To this order belong tapeworms with a scolex supplied with four suckers. There is no uterine pore; the genital pore opens laterally, the proglottids escape when mature, the eggs are not operculated, and the onchospheres are not ciliated. These are tænioid cestodes. Many of the more important human and other mammalian species belong to the family TÆNIIDÆ from which our type was selected (p. 230). Among these are *Tænia solium*, the pork tapeworm of man, *T. saginata*, the beef tapeworm of man, *T. pisiformis* of cats and dogs, *Echinococcus granulosus* (Fig. 166, c) of dogs and other carnivores which produces larval stages known as hydatids in man and other mammals. Common species belonging to other families are *Davainea tetragona* in domestic fowls, *Moniezia expansa* in sheep, *Hymenolepis nana* (Fig. 166, e), the dwarf tapeworm of man, *H. diminuta* of rats and mice and *Dipylidium caninum* of cats and dogs.

**Order 3. TETRAPHYLLIDEA.** — These cestodes have four lappet-like outgrowths from the scolex known as bothridia. The primary

uterine pore and one or more secondary uterine pores may or may not be present, and the eggs are not operculated. Reptiles, amphibians, fish, and elasmobranchs are parasitized by members of this order. *Calliobothrium verticillatum* occurs in the spiral valve of the smooth dogfish; *Crossobothrium laciniatum* in the sand shark, and *Echeneibothrium variabile* in the common skate.

**Order 4. TRYPANORHYNCHA.** — The scolex in this group is very long and consists of a head with two or four bothria and four retractile, spinose proboscides, and a long stalk. The genital pores are marginal. The larvæ encyst in teleost fish and the adults parasitize elasmobranchs. *Rhynchobothrius bulbifer* lives in the spiral valve of *Mustelus canis* and *Tetrahynchobothrium robustum* lives in the stomach and intestine of the skate.

The table on page 236 includes data regarding a few important tapeworms that live in man.

#### 4. CLASS IV. NEMERTINEA

There is considerable doubt as to the proper position of the NEMERTINEA in the animal kingdom but they are included here as a class of the PLATYHELMINTHES because they resemble other flatworms in certain respects.

The most important anatomical features of the NEMERTINEA (Fig. 167) are the presence of (1) a long proboscis, which lies in a proboscis sheath just above the digestive tract, and may be everted and used as a tactile, protective, and defensive organ; (2) a blood vascular system consisting usually of a median dorsal and two lateral trunks; and (3) an alimentary canal with both mouth and anal openings. The blood vascular system is here encountered for the first time. NEMERTINEA possess a mesoderm and nervous and excretory systems which do not differ markedly from those of the flatworms. The proboscis sheath may represent the coelom, but this is not certain.

Nemertines feed on other animals, both dead and alive. They live, as a rule, coiled up in burrows in the mud or sand, or under stones, but some of them frequent patches of seaweed. Locomotion is effected by the cilia which cover the surface of the body, by contractions of the body muscles, or by the attachment of the proboscis and subsequent drawing forward of the body. *Cerebratulus* swims actively like a leech. The power of regenerating lost parts is well developed.

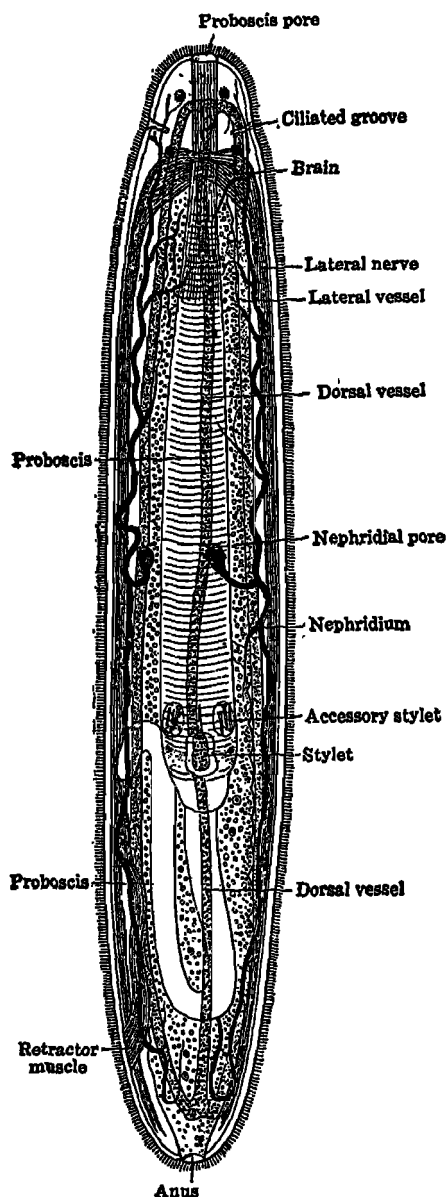


FIG. 167. — NEMERTINEA. *Tetrastemma*. General view of internal organs. (From Hatschek.)

During development a peculiar larval stage called the *pilidium* (Fig. 168) is usually passed through. This resembles a helmet with cilia on the surface and a long tuft of cilia at the apex. The adult develops from this larva by the formation of ectodermal invaginations which surround the alimentary canal. This invaginated portion escapes from the *pilidium* and grows into the adult nemertine.

The NEMERTINEA may be divided into three orders.

**Order 1. PALEONEMERTINI.** — The species in this order possess a proboscis free from stylets, and cerebral ganglia and lateral nerves in the ectoderm or between the two layers of muscles. *Carinella pellucida* is a marine species that lives below low water among annelid tubes and has been reported from Long Island and Vineyard Sounds and California. *Cephalothrix linearis* is another marine species living on both our Atlantic and Pacific coasts and in Europe.

**Order 2. METANEMERTINI.** — The proboscis in this group bears stylets and the lateral

nerves are in the muscle layers. The genus *Tetrastemma* (Fig. 167) is widespread and contains many species, mostly unisexual. They are small and possess four eyes. *T. candidum* is slender, about 2 cm. long, colored white, green, or yellow, and lives among algæ between tide lines on our eastern coast and in Europe. *Stichostemma rubrum* is a fresh-water species resembling *Tetrastemma*, but is about 18 cm. long, is yellow or reddish in color, and has three pairs of eyes. *Malacobdella grossa* is broad, has a sucker at the posterior end, and lives in the branchial chamber of pelecypod mollusks, such as *Mya* and *Venus*, on both sides of the North Atlantic.

### Order 3. HETERONEMERTINI.

— There are no stylets on the proboscis and the lateral nerve cords lie between

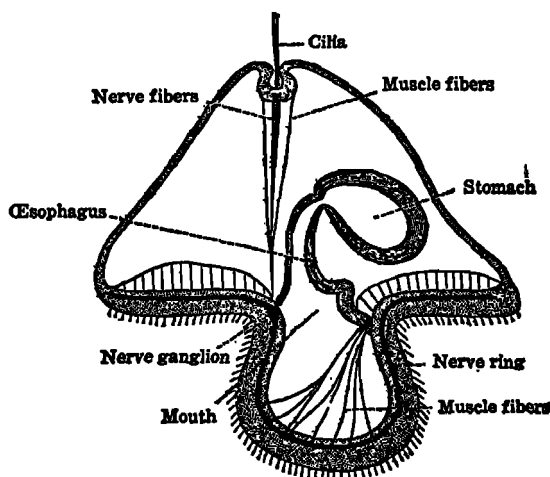


FIG. 168. — *Pilidium* larva of a nemertine. (After Salensky.)

layers of circular and longitudinal muscles. *Lineus ruber* (Fig. 170) has a long filiform body; is green, brown, or reddish in color; has a row of from four to eight eyes on either side of the head; and lives under stones in shallow water on our eastern coast, Alaska, and Europe. *Cerebratulus* is a well-known genus with representatives in all seas. *C. lacteus* may reach a length of several yards, is flesh color, has a white proboscis, and lives in the sand near low-water mark from Florida to Maine.

Several species of nemertines reproduce during the summer by spontaneous fragmentation (autotomy) followed by the regeneration of each of the two to twenty or more fragments into complete worms (Fig. 169). This type of reproduction is inhibited by cold weather in the autumn at the time when the sex cells are beginning to develop. Nemertines of these species possess remarkable powers of regeneration since, if, for example, an individual of

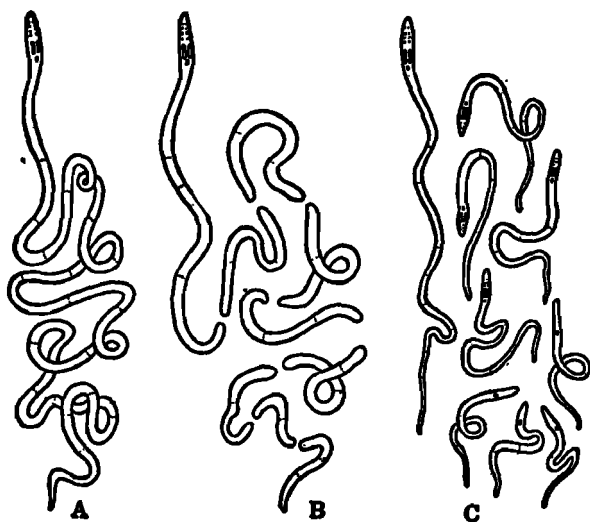


FIG. 169. — *Lineus socialis*: reproduction by fission. A, Mature worm. B, Worm divided by fission into nine pieces. C, Reconstruction of these pieces into complete worms. (From Coe.)

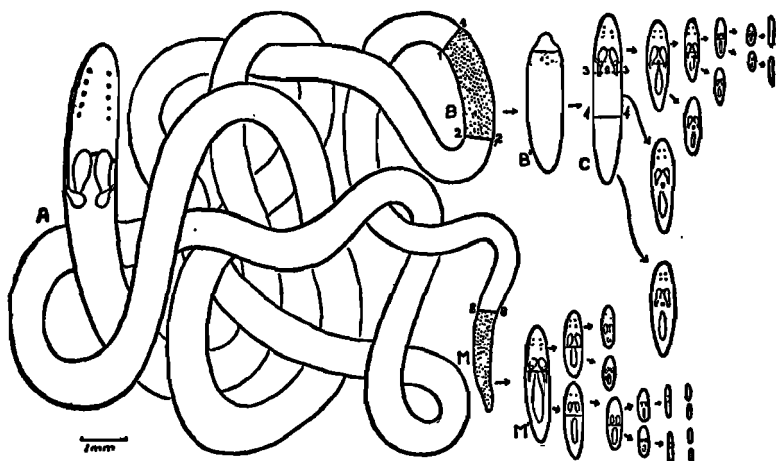


FIG. 170. — *Lineus socialis*: regeneration. A, normal worm; B, B', section cut from body and its appearance after twelve days; C, same after thirty days, cut in planes 3-3 and 4-4. Successive cuttings and regenerations indicated by arrows. M, M', similar experiments and results on posterior end of body. (From Coe.)

*Lineus socialis* 100 mm. in length is cut into as many as 100 pieces, each piece will regenerate a minute worm within four or five weeks. These minute worms may again be cut into pieces that regenerate and these may in turn be cut up and so on until miniature worms less than one two-hundred-thousandth the volume of the original worm result. (Fig. 170.)

## 5. PLATYHELMINTHES IN GENERAL

The flatworms differ greatly among themselves due largely to the fact that the TURBELLARIA are mostly free-living, whereas the TREMATODA and CESTODA are all parasitic in habit. The turbellarians, therefore, exhibit the typical organization of the group, the other two groups being modified considerably for a parasitic existence.

**External features.** — The PLATYHELMINTHES are flat and unsegmented, with definite anterior and posterior ends and bilateral symmetry. The ectoderm is ciliated in the TURBELLARIA, but in the TREMATODA and CESTODA the ectoderm is covered by a thick cuticle which it secretes, and cilia are absent. In some species sense organs are present.

**Body wall.** — Beneath the ectoderm are two layers of muscle, an outer layer of circular muscles and an inner layer of longitudinal muscles, except in the CESTODA; in this class the two layers are reversed. Between the body wall and the intestine is a mass of parenchymatous tissue (Fig. 151) which is very primitive in nature; it is of value in the reparation of lost parts and probably serves for the transportation of nutritive material. There is no coelom.

The nematocysts of *Hydra* are sometimes appropriated by a flatworm, *Microstomum caudatum* (Fig. 171). The worm eats and digests the *Hydra*, leaving the nematocysts free in the enteron. The endoderm cells of the worm engulf these nematocysts and pass them on to wandering mesenchyme cells which then become cnidophages. The nematocysts are uniformly distributed over the surface of the *Microstomum* within 12 hours after the ingestion of a *Hydra*. The worm appears to devour the *Hydra* not because of its food value but in order to secure the nematocysts which it employs, as does *Hydra*, as weapons of defense and offense. This is indicated by the fact that a worm already supplied with nematocysts does not attack *Hydra* readily although one with few



nematocysts does; that a worm with many nematocysts may retain the body of an ingested *Hydra* but egest the nematocysts, whereas a worm with few nematocysts may egest the body and retain the nematocysts; and that *Microstomum* has actually been seen to sting and paralyze other animals with the nematocysts obtained from *Hydra*. (Kepner and Barker)

**Digestive system.** — In the TURBELLARIA and TREMATODA there is a sac-like intestine with a single opening which serves both as mouth and anus. In the simplest forms the intestine is unbranched but in others, branches occur that may penetrate to all parts of

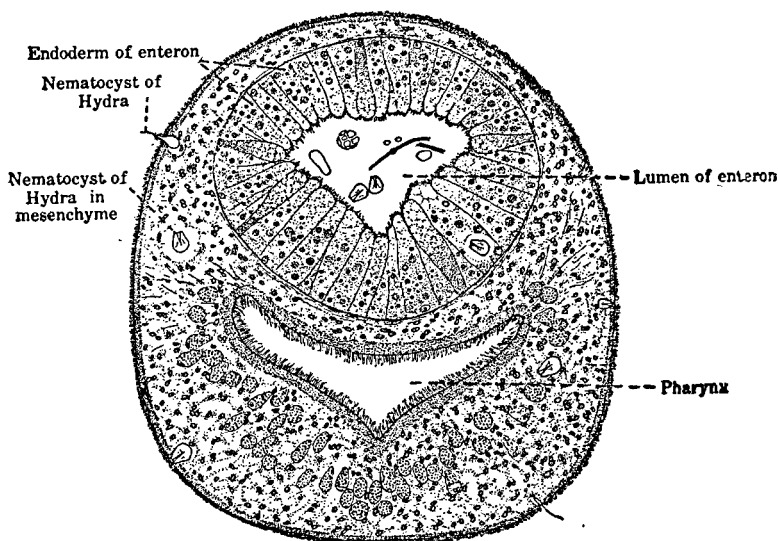


FIG. 171. — TURBELLARIA. *Microstomum caudatum*. Cross section through body near anterior end showing especially the location of nematocysts appropriated from hydras ingested as food. (After Kepner.)

the body thus rendering a circulatory system unnecessary. The CESTODA have lost the intestine and absorb nutriment through the general surface of the body. The NEMERTINEA possess both mouth and anus.

**Excretory system.** — An excretory system occurs in almost all of the flatworms and in some is very complicated. The most characteristic feature of this system is the flame cell.

**Nervous system.** — This consists of a network with a concentration of nervous tissue at the anterior end, forming the

cerebral ganglia, and several longitudinal nerve cords. Sense organs occur in free-living TURBELLARIA and may be present in the free stages of TREMATODA and CESTODA. They exist as eyes, otocysts, taste cells, tentacles, and ciliated ectodermal pits.

**Reproductive system.**—The flatworms are characterized by a complex reproductive system. The structure and differences have already been described for representatives of the classes. The trematodes and cestodes lay eggs more or less continuously but the turbellarians recognize the seasons in their reproductive activity. As noted above, the latter commonly multiply by asexual reproduction also.

In some TURBELLARIA, for example *Procotyla fluviatilis*, egg-laying proceeds during the entire year; in others, for example *Planaria alpina*, eggs are produced only during the winter months. Two different kinds of eggs are produced by *Mesostomum*; (1) "winter eggs" which have a thick shell, a large amount of yolk, escape only when the mother dies and remain dormant for a long period, and (2) "summer eggs" which have a thin shell, a small amount of yolk, escape from the living parent, and develop quickly.

**Embryology.**—The development of the egg of the polyclad, *Planocera inquilina*, has been worked out in detail (Surface, 1907) and an account of the embryology of this species is appropriate at this point. This flatworm lives in the mantle cavity of certain gastropods. The eggs are spherical and about one tenth of a millimeter in diameter. They are laid in spiral gelatinous capsules containing from 100 to 2000 eggs each. The early cleavage stages occur at intervals of about one hour. On the sixth day the larvæ break through the egg membranes and emerge as free-swimming organisms known as Müller's larvæ. These swim about for a time, and fall to the bottom where they change into the polyclad form.

**Cell lineage** (Fig. 172).—It is possible to follow the cleavage cells and their descendants from stage to stage until the larval condition is reached and in this way to ascertain the fate of each cell. Observations of this kind have been recorded for various types of animals and constitute what is called *cell lineage*. The egg of *Planocera* undergoes *total cleavage* into 2 and these into 4 cells (A). One of these 4, designated by the letter D, is larger than the other 3, which makes it possible to distinguish the

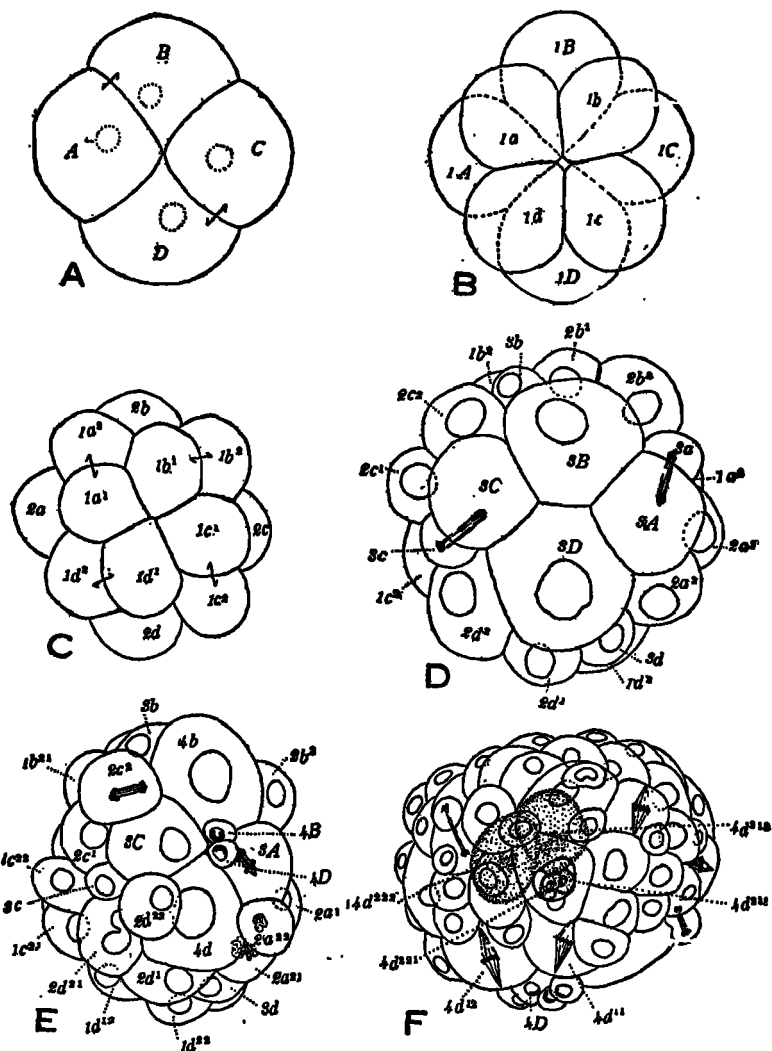


FIG. 172. — Cell Lineage of a Flatworm, *Planocera inquilina*. (From Sur-  
 ★ face.) A, Four-cell stage. B, Eight-cell stage with 4 macromeres (1A, 1B,  
 1C, 1D) and 4 micromeres (1a, 1b, 1c, 1d). C, Sixteen-cell stage viewed from  
 animal pole, showing three quartets of micromeres. D, Thirty-two-cell stage  
 viewed from vegetative pole, showing dextrotropic formation of 3a and 3c.  
 E, Thirty-six-cell stage viewed from near animal pole, showing especially  
 cell 4d. F, Stage with more than 100 cells, showing endoderm cells (4d<sup>11</sup>,  
 4d<sup>12</sup>, 4d<sup>211</sup>, 4d<sup>221</sup>) and mesoderm cells (4d<sup>212</sup>, 4d<sup>222</sup>).

different cells as cleavage advances. When the 4 cells, labeled *A*, *B*, *C*, *D*, divide to form 8(*B*), the 4 near the animal pole are smaller than the other 4; they are known as *micromeres* and labeled *1a*, *1b*, *1c*, and *1d*. At this stage, therefore, a quartet of micromeres are present and a quartet of larger, sister cells, called *macromeres* to which the labels *1A*, *1B*, *1C*, and *1D*, are applied. All of the cells that are descended from any cell of the 4-cell stage comprise a *quadrant*. The cleavage spindles during the division from the 4-cell to the 8-cell stage are oblique and the micromeres come to lie in the furrows between the macromeres, that is, alternate with them (*B*). This is known as *spiral cleavage*. In most cases when the egg is viewed from the animal pole, the micromeres lie in the furrow clockwise of the corresponding macromere; that is, cleavage is *dextrotropic* (*B*). Sometimes the micromeres lie in the furrow counter-clockwise of the corresponding macromere, in which case cleavage is said to be *laetotropic*.

The 8-cell stage develops into the 16-cell stage by the laetotropic division of the quartet of micromeres (*1c*, *1b*, *1c*, *1d*, to form *1a*<sup>1</sup>, *1a*<sup>2</sup>, *1b*<sup>1</sup>, *1b*<sup>2</sup>, *1c*<sup>1</sup>, *1c*<sup>2</sup>, *1d*<sup>1</sup>, *1d*<sup>2</sup>) and the production of a second quartet of micromeres (*2a*, *2b*, *2c*, *2d*) by the macromeres (*C*). The three quartets of micromeres present at this stage are destined to form the entire ectoderm of the animal, and the macromeres the endoderm and mesoderm. The 32-cell stage (*D*) is attained by the production of a third quartet of micromeres (*3a*, *3b*, *3c*, *3d*) by a dextrotropic division of the macromeres, and the division of each of the three quartets of micromeres. After the 32-cell stage division is not synchronous, and the various groups of cells must be considered separated.

Cell *4d*, which results from the division of macromere *D* at about the 40-cell stage, is of particular interest (*E*) since it gives rise to all of the endoderm (*4d*<sup>11</sup>, *4d*<sup>12</sup>, *4d*<sup>211</sup>, *4d*<sup>221</sup>) and part of the mesoderm (*4d*<sup>212</sup>, *4d*<sup>222</sup>). At about the 100-cell stage, *2a*<sup>112</sup>, *2b*<sup>112</sup>, *2c*<sup>112</sup>, and *2d*<sup>112</sup> are set aside as *mesoderm cells*. Primitive ganglion cells are recognizable at about this time (*1a*<sup>112212</sup>, *1b*<sup>112212</sup>, *1c*<sup>112212</sup>, *1d*<sup>112212</sup>).

**Phylogeny and interrelations.** — The flatworms, especially the TURBELLARIA, resemble the coelenterates in certain respects which indicate that they were derived from coelenterate-like ancestors. There is a single opening for the ingestion of food and egestion of waste material; a nerve net reminiscent of the coelen-

terates; and sense organs, such as otocysts, characteristic of coelenterates. The relation of flatworms to ctenophores is even more striking; polyclads being much like ctenophores that have adopted the creeping habit. In both groups the large macromeres produce ectoderm-forming micromeres; the nervous center is at the upper pole; an ectodermal stomodæum is at the lower pole; and the primary locomotor organs are eight ciliated bands forming comb of cilia in the adult ctenophore and in Müller's larva. The latter is what we may imagine the ctenophore-like ancestor of the polyclads to resemble. The principal differences between the different classes of flatworms appear to be due to the character of the habit, whether free-living or parasitic.

The history of our knowledge of the *Platyhelminthes*. — Parasitic flatworms, such as tapeworms, were well known to the ancients as inhabitants of man and domesticated animals. Trematodes were first described clearly in the sixteenth century but it was not until the close of the seventeenth century, that the hydatids of tapeworms were recognized as animals, having been considered previously as abscesses or abnormal growths. Linnæus placed all of the invertebrates except the arthropods into one class, the VERMES, and allocated the worms to an order, the INTESTINA, of this class. The fundamental difference between segmented and unsegmented worms was recognized by Cuvier in 1798. To the unsegmented worms Rudolphi in 1808 proposed the name ENTOMOZOA, because at that time most of the species known were internal parasites. Five orders were recognized by Rudolphi, (1) NEMATODES, (2) ACANTHOCEPHALA, (3) TREMATODES, (4) CESTODES and (5) CYSTICI. The term TURBELLARIA was coined by Ehrenberg in 1831 for the free-living species of flatworms because the beating of their cilia caused disturbances (turbellæ) in the water. Trembley in 1744 published the first figure of a turbellarian in his memoir on *Hydra*, and Borlase in 1758 gave us the first description of a nemertine (*Lineus*). O. F. Müller and Ehrenberg founded our knowledge of the TURBELLARIA and Lang and von Graff have contributed more recently. In 1851 Vogt united the four orders of flatworms in the class PLATELMIA which we now know as the phylum PLATYHELMINTHES. Leuckart, who contributed so much to our knowledge of the parasitic worms, presents the history of the subject up to the year 1879 in his book *The Parasites of Man*.

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## CHAPTER VI

### PHYLUM NEMATHELMINTHES

#### INTRODUCTION

The NEMATHELMINTHES are called unsegmented round worms, to distinguish them from the flatworms and segmented annelids. They are long, slender animals usually with a smooth and glistening surface and tapering somewhat toward one or both ends. Round worms are very widely distributed and occur in large numbers, both as regards species and individuals, in soil, fresh water and salt water, and as parasites in plants and animals. It has been estimated that the top six inches of an acre of arable soil contains thousands of millions of nemas. In size, they range from about one fiftieth of an inch to four feet in length. One can recognize most of them easily because of their peculiar movements. They whip about by contortions of their entire body in a dorso-ventral plane without making any forward progress unless solid particles are present for the body to lash against. As a rule, the free-living nemas are slighted in courses in zoology because they are mostly small and not of medical interest. However, they present the morphological and physiological characteristics of the phylum in certain respects better than do the parasitic species, which are modified more or less for their mode of life.

There is no satisfactory classification of the heterogeneous group of worms usually included in the phylum NEMATHELMINTHES. The following divisions are recognized largely for convenience.

**PHYLUM NEMATHELMINTHES.** — Unsegmented, triploblastic, bilaterally symmetrical animals; body cylindrical and elongate; no cilia; sexes usually separate.

**CLASS I. NEMATODA.** — With intestine but no proboscis.

**SUBCLASS I. EUNEMATODA.** — With body cavity lined with epithelium; gonads continuous with their ducts; no cloaca in female; lateral chorda present.

**Order 1. ASCAROIDEA.** — Free-living or parasitic; with three lips.

**Order 2. STRONGYLOIDEA.** — Parasitic; male with caudal bursa supported by rays; oesophagus club-shaped and without posterior bulb.

**Order 3. FILARIOIDEA.** — Parasitic; with paired lateral lips or with or without lip-like structures; oesophagus without bulb, the anterior portion muscular and posterior glandular.

**Order 4. DIOCTOPHYMOIDEA.** — Parasitic; body sometimes spiny; oesophagus long and club-shaped.

**Order 5. TRICHINELLOIDEA.** — Parasitic; oesophageal portion of body more or less distinct; oesophagus a cuticular tube embedded in a single row of cells.

**SUBCLASS II. GORDIACEA.** — With body cavity lined with epithelium; gonads not continuous with their ducts; cloaca present in female; lateral chorda absent.

**CLASS II. ACANTHOCEPHALA.** — Without intestine but with spiny proboscis.

## 1. CLASS I. NEMATODA

### (1) *TURBATRIX (ANGUILLULA) ACETI* — THE VINEGAR EEL

The vinegar eel, *Turbatrix aceti*, is a favorable free-living nematode for study because it is easily procured at any time of the year in cider vinegar, can be examined in the living condition and fixed and stained easily. It is visible to the naked eye when held before a bright light and exhibits characteristic nematode movements. Heating for a minute kills and straightens vinegar eels, and staining with Delafield's hæmatoxylin in 70 per cent alcohol reveals the internal organs.

The worms are cylindrical, the anterior end being slightly narrowed and the posterior end tapering to a fine point. The female is about 2 mm. in length and 0.05 mm. in breadth and the male about 1.4 mm. in length and 0.03 mm. in breadth. The *cuticle* is transparent and transversely striated. The *mouth* is a pore at the anterior end; it opens into a cone-shaped *buccal capsule* about 0.01 mm. long. The posterior portion of the buccal capsule is provided with one dorsal and two ventro-lateral *teeth*. The *oesophagus*, in which the buccal capsule is partly embedded, consists of an anterior thick portion 0.1 mm. in length, followed by a narrow neck 0.05 mm. in length which leads to a muscular bulb 0.02 mm. in diameter in which is a valvular apparatus. The *ex-*



*cretory pore* is difficult to find; it is on a level with the anterior end of the bulb. Just in front of the bulb, the *nerve ring* crosses the *oesophagus*. The *intestine* is a straight tube, about 0.02 mm. in diameter in the female and smaller in the male; it extends from the *oesophagus* to the *rectum*, which is short, narrow, and straight and opens into the *cloaca*.

The *male reproductive organs* consist of a testicular tube, a seminal vesicle, a genital pore, a pair of spicules, and an accessory piece. The *testicular tube* forms a loop arising about 0.3 mm. from the ano-genital pore, extending forward about 0.1 mm. and then bending back upon itself to the *genital pore* which opens into the *cloaca*. It contains reproductive cells in two or three rows near its origin but these form a single row from near the bend to the posterior end. A portion of the tube near the posterior end is modified into a thin-walled *seminal vesicle* in which spermatozoa may be seen. This joins the rectum to form a short *cloaca*. Near the opening of the *cloaca* to the outside is a pair of *curved spicules* about 0.37 mm. long and an accessory piece, which is a curved plate shaped somewhat like the keel of a boat. The muscles that extend the spicules are conspicuous. Five pairs of *papillæ* are present near the cloacal opening; one postanal, dorsal pair; two preanal, ventral; one adanal, ventral; and one postanal, ventral.

The *female reproductive organs* comprise an ovarian tubule, a seminal receptacle, a uterus, a vagina, and vulva. The *ovarian tubule* arises posterior to the middle of the body, runs forward dorsally about 0.5 mm. where it joins the *uterus* which runs backward ventrally to the vagina which opens to the outside through the slit-like *vulva* near the middle of the body. An oval sac extending posteriorly from the vulva is probably a *seminal receptacle*. The ovarian tubule contains a single row of germ cells; these are fertilized near the bend where they become oval in shape and soon begin to segment. A varied number of *eggs* may be present in the uterus but usually about two ovoid and three vermiform embryos may be observed. The thin egg membrane ruptures in the uterus and the young are born in an active condition, that is, the vinegar eel is viviparous. The fertilized eggs hatch in about eight days, and the larvæ, which are 0.2 mm. long when hatched, become mature in about four weeks. Males and females are equal in number; they may live for ten months or more and one female may produce as many as forty-five larvæ.

(2) METONCHOLAIMUS  
PRISTIURUS

This free-living nematode occurs at Woods Hole, Mass., and in the Mediterranean Sea in stagnant marine mud, below low tide, often under eelgrass. It is included here since it possesses certain structures not exhibited by the vinegar eel or parasitic nematodes and can be obtained from the supply department of the Marine Biological Laboratory at Woods Hole, Mass.

## External features (Fig. 173).

— The *cuticle* is thin and transparent with transverse striæ (usually not visible). The *head* is blunt with a centrally located *mouth*. The *neck* includes about one tenth of the animal and contains the *œsophagus*. *Setæ* are present on the head (4 pairs and 2 single) and a few of small size on the body and at the posterior end. Six mobile *lips* surround the mouth but can be counted only from in front. On either side of the head is a shield-shaped organ (*amphid*) connected with an interior pocket, probably of chemical sense. The *tail* is pointed and ends in a *spinneret* connected with glands that secrete a non-water-soluble cement used to fasten the tail to solid objects. Around the spinneret are inconspicuous *setæ*.

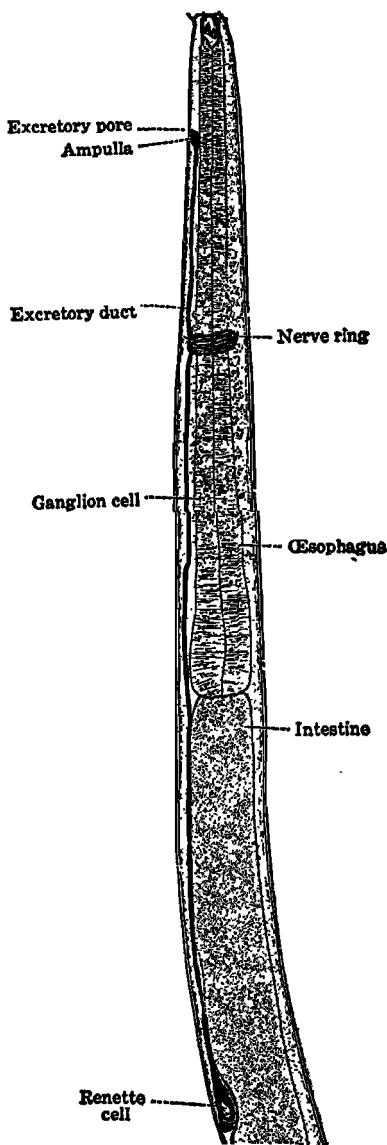


FIG. 173. — NEMATODA. *Oncholaimus pristiurus*. Anterior end. (After Chitwood.)

**Internal organs (Fig. 174).** — The mouth opens into a concave *pharynx* about 0.04 mm. long; this leads into the cylindrical *oesophagus*. The *intestine* is a straight tube with a wall consisting of a single layer of cells; within it can be seen the contents consisting of mud from which organic material is extracted. The *rectum* is short and opens to the outside through the *anus* near the posterior end of the animal. On the ventral side of the neck close to the head is an *excretory pore*, the opening of a single glandular cell. Passing around the *oesophagus* is a *nerve ring*, anterior and posterior

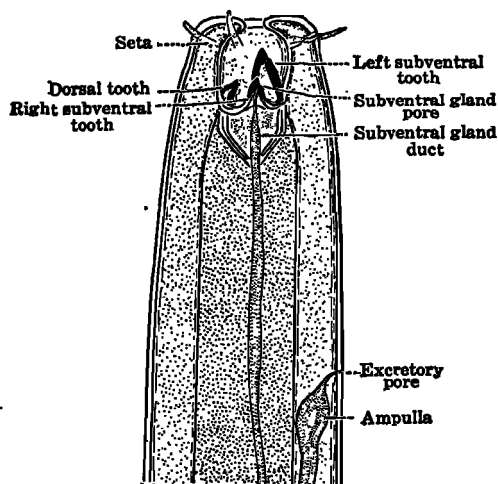


FIG. 174. — NEMATODA. *Oncholaimus pristiurus*.  
Lateral view of head. (After Chitwood.)

to which are ganglion cells. On either side of the body just beneath the cuticle is a wide ribbon-like *lateral cord*.

**Female reproductive organs.** — The female germ cells are contained in an *ovarian tubule* which leads to an *oviduct* and then into a straight *uterus* in which is a single row of eggs numbering up to forty. The eggs are fertilized when they enter the uterus and spermatozoa are pres-

ent at this point. Polar-body formation can be observed in the uterus, the polar bodies being visible just beneath the smooth egg-shell. The eggs do not segment before they are laid. A system of efferent tubes, the *demanian system*, opens a short distance anterior to the anus through a pore; these tubes secrete an elastic, sticky, non-water-soluble substance probably of use during copulation or for the protection of the eggs. The *vulva*, through which the eggs pass to the exterior, is a transverse slit near the middle of the animal.

**Male reproductive organs.** — The male germ cells are contained in two straight *testicular tubules* which extend backward and forward in opposite directions from near the middle of the body where they unite in the *vas deferens*. An accessory gland pours its

secretion into the vas deferens. The spermatozoa are carried from the vas deferens into the *ejaculatory duct*. Two colorless, long, slender *spicules* with retractor and protrusor muscles aid in transferring the spermatozoa to the female. The male possesses a small preanal papilla and a row of about ten supplementary organs on the ventral, posterior part of the tail which give it a serrated appearance, hence the species name *pristiurus* (saw-tailed). Two rows of about thirty minute *setæ*, sensory in function, extend forward from near the end of the tail and surround the anus.

### (3) ASCARIS LUMBRICOIDES

**External features.** — *Ascaris lumbricoides* is the common round worm parasitic in the intestine of man. Round worms morphologically indistinguishable from this species occur in pigs, but these have been shown to be physiologically different and not infective to man. The sexes are separate. The female, being the larger, measures from five to eleven inches in length and about one fourth of an inch in diameter. The *body* when alive, may be milk-white or somewhat reddish-yellow in color, and has a characteristic sheen; it has a dorsal and a ventral narrow white stripe running its entire length and a broader *lateral line* is present on either side. The *cuticula* is smooth and marked with fine striations. The *mouth* opening is in the anterior end and is surrounded by one dorsal and two ventral *lips*; these are finely toothed and bear *papillæ*, the dorsal lip two and each ventral lip one. Near the posterior end is the *anal opening*, from which, in the male, extends two spicules or *penial setæ* of use during copulation. Many ventral preanal and postanal *papillæ* are also present in the male. The male can be distinguished from the female by the presence of a bend in the posterior part of the body. In the female, the genital opening, the *vulva*, is located about one third of the length of the body from the anterior end.

**Internal anatomy.** — If an animal is cut open along the dorsal line (Fig! 175), it will be found to contain a straight *alimentary canal*, and certain other organs, lying in a central cavity, the *celom*, a cavity met with now for the first time. The alimentary canal is very simple, since the food is taken from material already digested by the host whose intestine the worm inhabits. It opens at the posterior end through the *anus*, which is not present in members of the phyla already discussed. A small *buccal vestibule*

opens into the muscular *oesophagus*, from 10 to 15 mm. long, which draws the fluids into the long non-muscular intestine through the

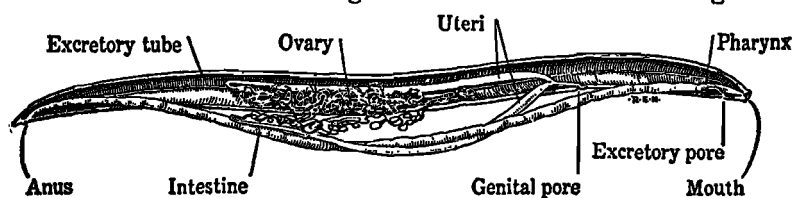


FIG. 175. — *Ascaris lumbricoides* female: dissection to show internal organs. (From Woodruff.)

walls of which the nutriment is absorbed. Just before the anal opening is reached, the intestine gradually becomes smaller; this

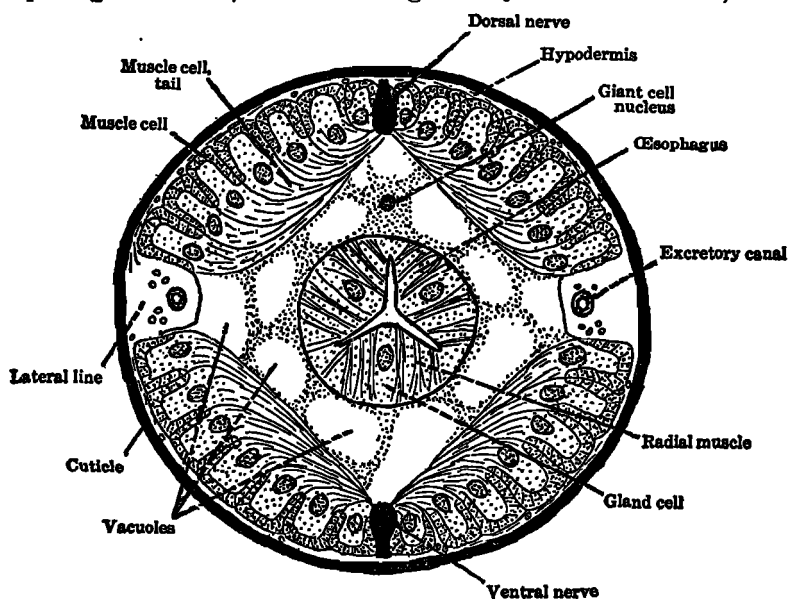


FIG. 176. — NEMATODA. *Ascaris*. Cross section of body through region of oesophagus. (After Borradaile and Potts, modified.)

portion is known as the *rectum*. The rectum opens through the *anus* in the female and into the *cloaca* in the male.

The *excretory system* consists of two longitudinal canals (Fig. 176), one in each lateral line; these open to the outside by a single pore situated near the anterior end in the ventral body wall.

A ring of *nervous tissue* surrounds the oesophagus and gives off

two large nerve cords, one dorsal, the other ventral, and a number of other smaller strands and connections.

The *male reproductive organs* are a single coiled thread-like *testis*, from which a *vas deferens* leads to a wider tube, the *seminal vesicle*; this is followed by the short muscular *ejaculatory duct* which opens into the cloaca. In the *female* lies a Y-shaped reproductive system. Each branch of the Y consists of a coiled thread-like *ovary* which is continuous with a larger canal, the *uterus*. The uteri of the two branches unite into a short muscular tube, the *vagina*, which opens to the outside through the *genital aperture* or *vulva*. *Fertilization* takes place in the uterus. The egg is then surrounded by a shell of chitin, and passes out through the genital pore. The genital tubules of a female worm may contain as many as 27 million eggs at one time and each mature female lays about 200,000 eggs per day.

The relations of the various organs to one another, as well as the structure of the body wall, and the character of the coelom, are shown in figure 176, which is a transverse section of a female specimen of *Ascaris lumbricoides*. The body of the worm should be considered as consisting of two tubes, one, the intestine, lying within the other, the body wall; while between them is a cavity, the *coelom*, in which lie the reproductive organs.

The *body wall* is composed of several layers, an outer chitinous cuticle, a thin layer of ectoderm just beneath it, and a thick stratum of longitudinal muscle fibers, mesodermal in origin, lining the coelom. Thickenings of the ectoderm form the dorsal, ventral, and lateral lines. In each of the last-named lies one of the longitudinal excretory tubes. The nerve cords are also embedded in the body wall.

The *intestine* consists of a single layer of columnar cells, the endoderm, coated both within and without by a thin cuticle.

The *coelom* of *Ascaris* differs from that of the higher animals in several respects. Typically the coelom is a cavity in the mesoderm lined by an epithelium; into it the excretory organs open, and from its walls the reproductive cells originate. In *Ascaris* the so-called coelom is lined only by the mesoderm of the body wall, there being no mesoderm surrounding the intestine. Furthermore, the excretory organs open to the exterior through the excretory pore, and the reproductive cells are not derived from the coelomic epithelium. The body cavity of *Ascaris*, therefore, differs structurally and

functionally from that of a true coelom, but nevertheless is similar in many respects.

**Life cycle.** — Maturation, fertilization, and the phenomena concerned with the early differentiation of germ cells and somatic cells in *Ascaris* eggs have for many years served to illustrate these processes in animals in general. The eggs of *Ascaris* segment after they leave the body. They are very resistant and may remain alive in the soil for months. Embryos are formed under favorable conditions in about two weeks. Infection with *Ascaris* results from ingesting embryonated eggs. The eggs are usually carried to the mouth either with food or water or by accidental transfer of soil containing such ova. They do not regularly hatch in the stomach but pass to the small intestine where they begin to hatch within a few hours after ingestion. Formerly it was believed that the larvæ upon hatching settled down in the small intestine and there developed directly into the adult stage. Recent investigations have shown, however, that the larvæ of this parasite leave the intestine immediately after hatching and then follow a definite path of migration through the tissues of the host, afterward returning to the intestine to grow into mature worms.

The newly hatched larvæ burrow into the wall of the intestine and enter the lymphatic vessels or the venules. If the larvæ enter the lymphatics they are carried to the mesenteric lymph nodes and from there may reach the circulation either by entering the blood capillaries and passing into the portal circulation, or pass into the thoracic duct and from there to the right side of the heart. If the portal circulation is entered the larvæ are carried to the liver where they pass from the interlobular veins to the intralobular veins. From the liver they are carried to the right side of the heart and then to the lungs. Within the lungs they break into the alveoli where some further development and growth takes place, after which they pass on to the intestine by way of the trachea, cesophagus, and stomach. This journey through the host's tissues requires about ten days. They become mature worms in the intestine in about two and one half months.

**Relations of *Ascaris* to man.** — Ascarids are pathogenic to man. When large numbers of larvæ pass through the lungs inflammation is set up and generalized pneumonia may result. The adults may be present in the intestine in such large numbers as to produce intestinal obstruction and nervous symptoms may appear as a

result of the secretion of toxic substances by the worms. Fortunately several drugs are available which easily remove the worms; the best of these are oil of chenopodium and hexyl resorcinol. Ascariasis is essentially a children's disease. Recently in southwestern Virginia 60 per cent of the children and 30 per cent of the adults in a community were found to be infected. The infestation was particularly severe in families where the children were allowed to pollute the soil near the houses. Under these conditions the soil contains large numbers of embryonated eggs which find their way into the children's mouths on dirty hands. Infection can be prevented easily by enforcing sanitary practices.

#### (4) OTHER NEMATODA

**Nematodes.** — As stated in the introduction to this chapter, it seems advisable to include the *EUNEMATODA* and *GORDIACEA* as subclasses in the class *NEMATODA*. Almost all of the free-living *EUNEMATODA* belong to the order *ASCAROIDEA*; the parasitic species belong to this order and to the other four orders recognized.

**Free-living Nematodes.** — Round worms that are not parasitic are more abundant and more widely distributed on the earth's surface than most zoologists realize. They live in almost every conceivable type of environment, such as in wet sand or mud, aquatic vegetation, in standing or running water, in the soil, the sea, tap water, fruit juices, and in moist places almost everywhere. "If all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes, and oceans represented by a film of nematodes. The location of towns would be decipherable, since for every massing of human beings there would be a corresponding massing of certain nematodes. Trees would still stand in ghostly rows representing our streets and highways. The location of the various plants and animals would still be decipherable, and, had we sufficient knowledge, in many cases even their species could be determined by an examination of their erstwhile nematode parasites." (Cobb.) Free-living nematodes are mostly small, a large specimen being only one cm. in length. The eggs may withstand dessication, a fact which no doubt is responsible in part for their wide distribution, since they may be carried about by the



wind as well as by currents of water, birds and other animals, and by man. They feed on other nematodes and on microorganisms. Most species are transparent but some have pigment granules in the intestinal cells which give them a yellowish or brownish appearance. Colored eye spots may also be present.

The body is covered by a transparent non-cellular coat, the cuticula, beneath which is a cellular layer, the subcuticula or hypoderm, which secretes the cuticula. The cuticula is shed about four times during the growth of the larva and the lining of the mouth, œsophagus, and rectum are shed at the same time. Within the cells of the hypoderm are longitudinal contractile fibers. The hypoderm is in many nematodes thickened along the center of the lateral and dorsal and ventral surfaces thus dividing the body wall into four quadrants. The thickenings on the sides are called lateral lines. The digestive system is simple. The mouth is at the anterior end, usually surrounded by lips or papillæ. Teeth may be present for rasping the tissue of plants or animals on which the nematodes feed. The buccal cavity or pharynx is tubular, funnel-shaped, or expanded into a cup-shaped capsule adapted for sucking. The œsophagus is either a thin-walled tube, or thick and muscular, and usually possesses a bulb or valvular apparatus where it joins the intestine. The intestine is a straight tube of columnar epithelial cells. It decreases in size at the posterior end in the female, becoming the rectum. In the male the intestine and genital duct open into a cloaca. The anal opening is on the ventral surface near the posterior end.

The excretory organ is a unicellular gland, the renette, located in the body cavity near the union of œsophagus and intestine. A nerve ring surrounds the œsophagus. Certain species possess a pair of pigmented eye spots, one on either side of the œsophagus. Cephalic, caudal, and terminal setæ, probably organs of touch, taste, or smell, occur on free-living but not on the parasitic species. A pair of laterally situated cephalic organs known as amphids, probably sensory in nature, also occur on free-living nemas. The free-living stages of certain parasitic nematodes also possess sensory organs. No circulatory system is present, circulation being accomplished by the fluid in the body cavity in which currents are set up by the movements of the worm. The sex organs are, in general, similar to those of *Turbatrix* and *Metoncholaimus* already described.

Some of the families that contain free-living nematodes are as follows:

**RHABDITIDÆ.** — This family is discussed later.

**MERMITHIDÆ.** — The adults live in fresh water or in the ground. The larvæ are at first free-living but complete their development in the body cavity usually of an insect or mollusk. Example, *Mesomermis virginiana* from a cranberry bog in Virginia.

**TYLENCHIDÆ.** — Parasitic and semi-parasitic as well as free-living species belong to this family. Example, *Iota octangulare* from Dismal Swamp, Virginia.

**TRILOBIDÆ.** — These are all free-living and mostly marine. Examples, *Trilobus longus*, from mud at the base of aquatic plants in fresh water throughout the United States; *Monhystera sentiens*, a species of a widespread genus living in salt water or the soil.

**ALAIMIDÆ.** — Mostly marine species but sometimes inhabitants of fresh water or earth. Example, *Bastiania exilis* from fresh water, a species of a genus with representatives in America, Europe, Japan, and Australia.

**CHÆTOSOMATIDÆ.** — Free-living species marine in habit. Example, *Chætosoma ophicephalum*.

**DESMOSCOLECIDÆ.** — Marine, free-living species. Example, *Desmoscolex minutus*.

**ONCHOLAIMIDÆ.** — Free-living in fresh and salt water and in soil. Examples, *Metoncholaimus pristiurus* (Fig. 173), from stagnant marine mud; *Mononchus major*, a member of a genus containing many fresh-water and soil-inhabiting species that feed on other nematodes.

**Parasitic Eunematoda.** — The members of this group are modified in certain respects for a parasitic existence but resemble the free-living species in their fundamental structure. Some of them, such as *Strongyloides*, may pass through a free-living stage; others such as *Rhabditis* (Fig. 177), may apparently live either a free or parasitic existence. Most of them, however, are obligatory parasites restricted to a single host species. Life outside of the body of the host may be passed entirely in the egg, as in *Ascaris* and *Trichuris*, or the eggs may hatch, as in the hookworm, and the larvæ that escape may infect new hosts. An intermediate host is required for the complete life cycle of some species, such as the guinea worm, which passes through certain stages in man and the rest in the crustacean, *Cyclops*. The types of variations in the life

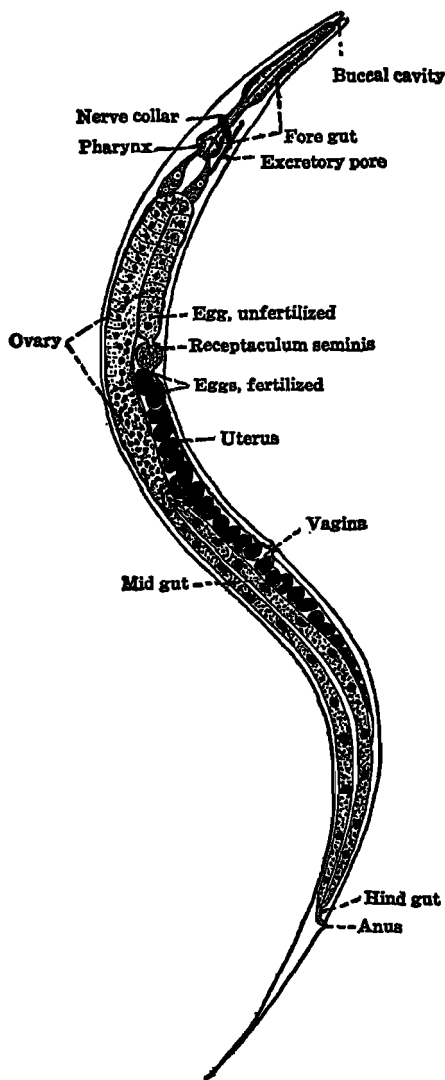


FIG. 177. — NEMATODA. *Rhabditis*. Mature female. (After Maupas, modified.)

cycles are indicated in the brief descriptions of certain important species presented below.

It is convenient to recognize five orders of EUNEMATODA as indicated on page 248. Hundreds of interesting and important species might be described but because of lack of space only a few that live in man or in lower animals can be mentioned.

#### Order ASCAROIDEA. —

Species belonging to four families may be included here. The family ASCARIDÆ includes among others the genera *Ascaris* and *Toxocara*. Species of *Ascaris* are parasites of mammals, having been reported from cattle, skunk, and armadillo. *Ascaris lumbricoides*, described in section 4 of this chapter, has been reported from man, monkey, pig, and squirrel. The genus *Toxocara* contains species parasitic in carnivores and elephants. *Toxocara canis* is the common ascarid of dogs being especially prevalent in puppies. Dogs become infected by swallow-

ing the eggs. The larvæ migrate through the body as do those of *Ascaris lumbricoides* in man. Dogs acquire an immunity as a result of the infection and after three or four months the worms are cast out and susceptibility to further infection is lost.

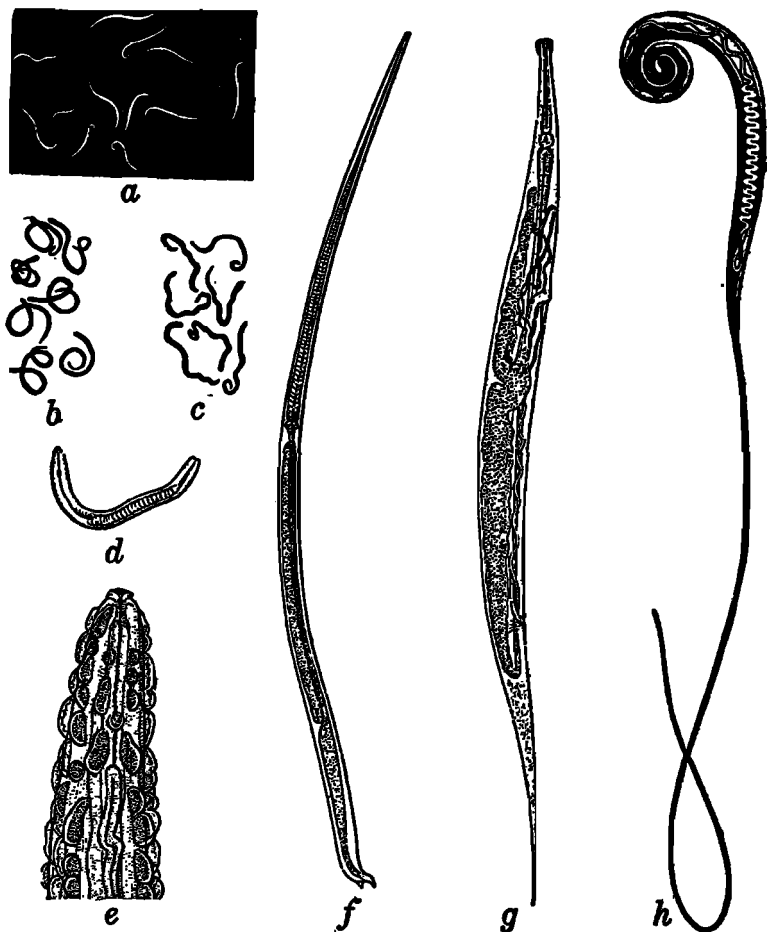


FIG. 178. — NEMATODA. a, *Heterakis gallinae*, from the cæcum of fowls; about  $\frac{1}{2}$  natural size. b, *Wuchereria bancrofti*, microfilariae. c, *Loa loa*, microfilariae. d, *Trichinella spiralis*, the trichina worm, young larva. e, *Gongylonema pulchrum*, anterior end, from man. f, *Trichinella spiralis*, the trichina worm, male. g, *Enterobius vermicularis*, female; the pinworm of man. h, *Trichuris ovis*, whipworm, from sheep and cattle. (After various authors.)

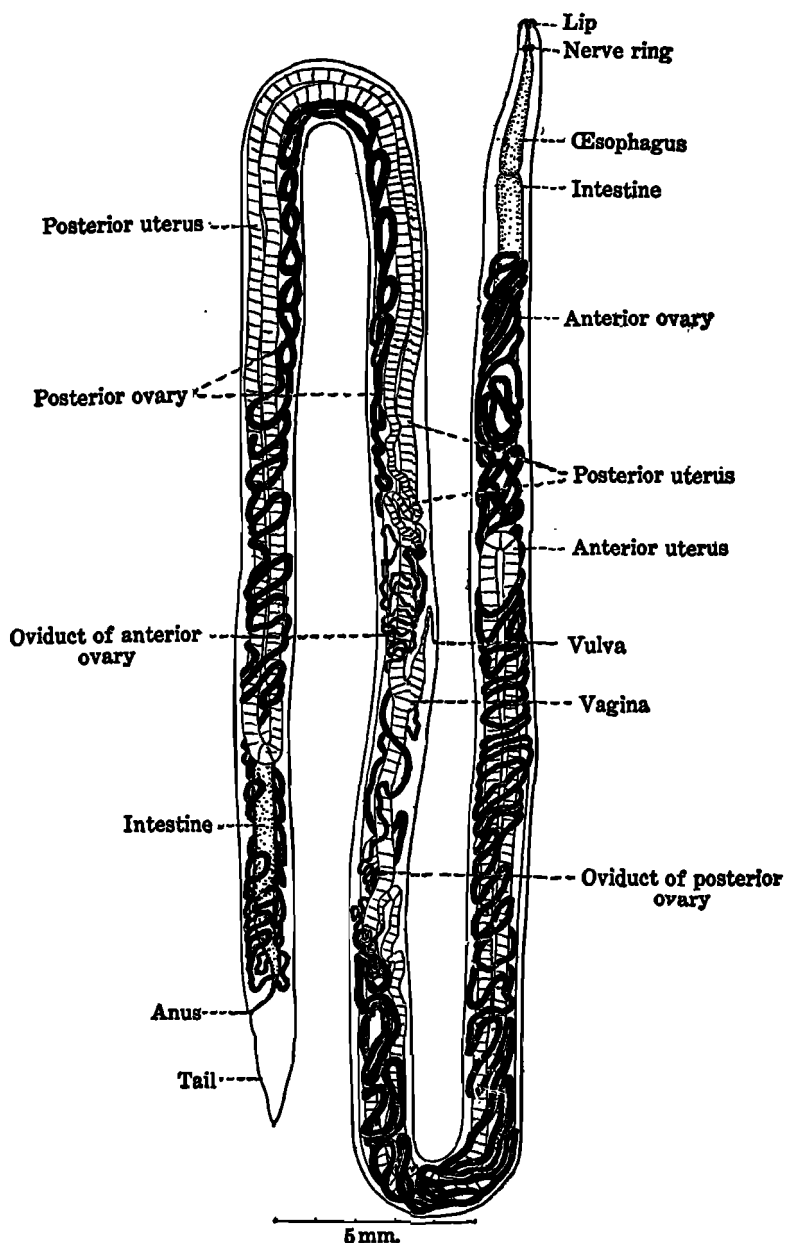


FIG. 179. — NEMATODA. The chicken nematode, *Ascaridia lineata*, female. Digestive and reproductive organs. The uterus is distinguished from the other organs by cross lines. (After Ackert, modified.)

Two genera of the family HETERAKIDÆ will be referred to here. *Heterakis* contains species that live in birds and mammals. Of particular importance is *Heterakis gallinæ* (Fig. 178, a) which lives in the cecum of barnyard and wild fowls. Eggs, which are passed in the fæces of infected birds, are swallowed and the young that hatch from them in the small intestine move on into the ceca. They do not seriously injure the fowls but are of great economic importance since they carry with them a protozoan parasite, *Histomonas meleagridis*, which is the causative agent of the disease of turkeys known as blackhead. *Ascaridia lineata* (Fig. 179) is the common round worm of chickens, living in the small intestine.

To the family OXYURIDÆ belong the pinworm of man, *Enterobius vermicularis* (Fig. 178, g) and a similar species in horses. The human pinworm (female) measures from 9 to 12 mm. in length, is world-wide in distribution and lives in the adult stage in the upper part of the large intestine. Children are often infected, sometimes over 5000 worms being present in a single child. The female worms creep out of the rectum, usually at night, causing intense itching. They lay their eggs at once. The infected person scratches the anal region thereby contaminating the hands, especially the finger-nails, and the eggs are then conveyed to the mouth and swallowed, thus increasing the infection. Carbon tetrachloride is an effective remedy. *Oxyuris equi* resembles the pinworm of man; it causes anal pruritus in horses, asses, and mules.

Species in the family RHABDITIDÆ may be entirely free-living or entirely parasitic or may pass part of the life cycle as a free-living worm and the rest as a parasite. *Rhabditis hominis* (Fig. 177) is a coprozoic species that has been reported as an occasional human parasite. *Strongyloides stercoralis* is a common human parasite especially in the moist tropics. Its life cycle includes a female stage that lives in the human intestine and lay eggs that give rise to male and female larvæ. These rhabditiform larvæ pass out in the fæces and form a free-living generation. They may become infective larvæ or develop into sexually mature adults. The offspring of these are filariform larvæ which are infective to man. They may be swallowed but usually penetrate the skin of bare feet. They are carried in the blood stream to the lungs, break out into the trachea, migrate through the epiglottis into the digestive tract, and become localized in the ileum.

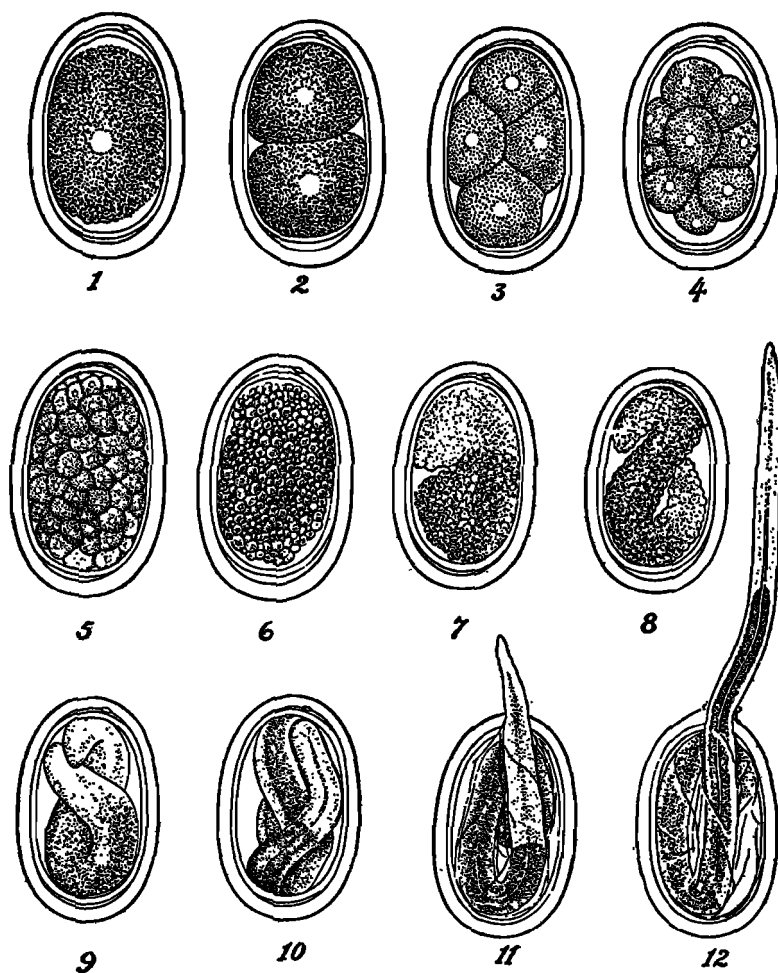


FIG. 180. — NEMATODA. Development of the egg of the chicken nematode, *Ascaridia lineatus*. 1, Fertilized egg. 2, Two-cell stage. 3, Four-cell stage. 4, Early morula stage. 5 and 6, Late morula stages. 7, "Tadpole" stage. 8 and 9, Vermiform stages. 10, Coiled embryo = "embryonated egg." 11 and 12, Young worm hatching. (After Ackert.)

**Order STRONGYLOIDEA.** — Many interesting and economically important species belong to this order. Four of the seven families will be mentioned here. The family STRONGYLIDÆ contains many parasites of domesticated animals. *Strongylus vulgaris* is the most important round worm of horses and other EQUIDÆ and is world-

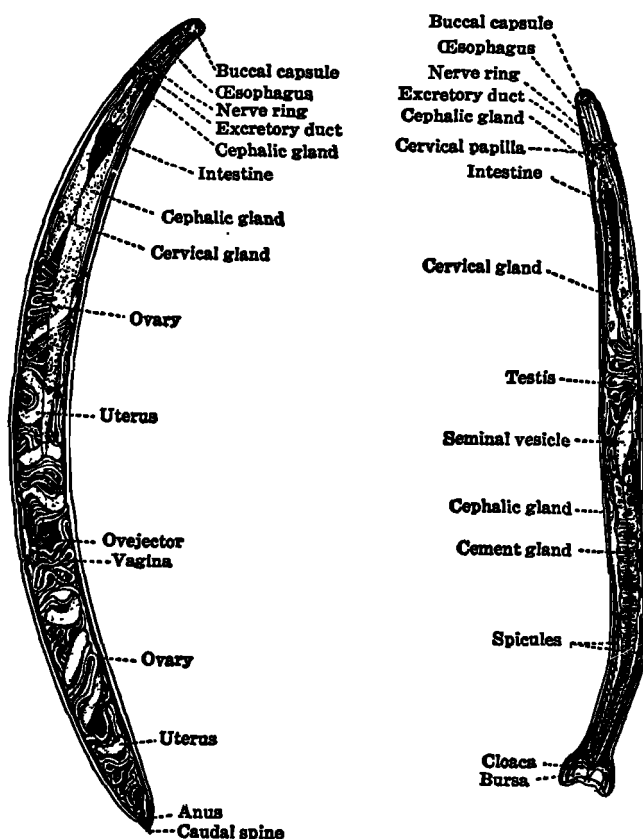


FIG. 181. — *Ancylostoma duodenale*, the Old World Hookworm, female (left) and male (right). (After Loos.)

wide in distribution but especially prevalent in warm countries. It lives in the cecum or colon attached by the mouth to the mucosa, from which it sucks blood. Loss of blood results in anæmia. The eggs of *Strongylus* are deposited in the fæces where they give rise to infective larvæ. These, when ingested by a horse, migrate to the posterior mesenteric artery where an aneurysm is produced;



they then move on to the cecum where they become encysted in the submucosa; and finally they break out into the lumen, attach themselves to the mucosa, and develop into adults. Oil of chenopodium is recommended to remove worms from the intestine.

The nodular worm of sheep and goats, *Oesophagostomum columbianum* also belongs to this family. The young worms encyst in the wall of the intestine forming nodules. Later they break out

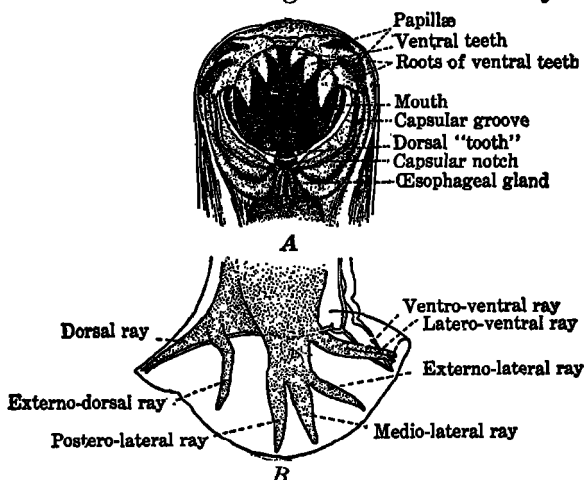


FIG. 182. — Hookworm. A, Buccal capsule of *Ancylostoma caninum*, the dog hookworm. B, Bursa of *A. duodenale*, the human hookworm. (A, from Chandler; B, after Loos.)

into the lumen and become adults. Diarrhea and emaciation result from infection and the intestines are not usable for sausage casings. No treatment is known. Another strongyl of importance is *Syngamus trachea*, a slender red worm which occurs in the trachea of fowls and wild birds and causes gapes. Infection results from the ingestion of infective larvæ that hatch from eggs passed in the fæces or coughed up by infected birds. The larvæ penetrate the wall of the oesophagus, migrate to the lungs, where they become mature, and later move into the trachea to the wall of which they attach themselves by the buccal capsule. Fowls suffer from catarrh and from abscesses where the worms are attached.

The hookworms belong to the family ANCYLOSTOMIDÆ. The hookworm of the Old World is *Ancylostoma duodenale* (Fig. 181). Other species of this genus occur in the intestine of various species of carnivores including the dog, cat, tiger, lion, and wolf. The

hookworm of the New World is *Necator americanus* which lives in man and pig. Other species of *Necator* have been reported from chimpanzees. The larvæ of the hookworm develop in moist earth and usually find their way into the bodies of human beings by boring through the skin of the foot. In the localities where the hookworm is prevalent, many of the people go barefoot. The larval hookworms enter the veins and pass to the heart; from the heart they reach the lungs, where they make their way through the air passages into the windpipe, and thence into the intestine. To the walls of the intestine the adults attach themselves and feed upon the blood of their host (Fig. 183). In the case of the dog hookworm and probably also of the human hookworm, blood is continuously being sucked into the body of the worm and expelled from the anus in the form of droplets consisting mainly of red corpuscles. Calculations indicate the possibility that a single worm may withdraw blood from the host at the rate of 0.8 cc. in 24 hours. (Wells.) When the intestinal wall is punctured, a small amount of poison is poured into the wound by the worm. This poison prevents the blood from coagulating, and therefore results in a considerable loss of blood, even after the worm has left the wound. The victims of the hookworm are anæmic, and also subject to tuberculosis because of the injury to the lungs. It is estimated that 2,000,000 persons are afflicted by this parasite in the United States. Hookworm disease can be cured by oil of chenopodium, carbon tetrachloride, or tetrachlorethyl. The most important preventive measure is the disposing of the human fæces in rural districts, mines, brick-yards, etc., in such a manner as to avoid pollution of the soil, thus giving the eggs of the parasites contained in the fæces of infected human beings no opportunity to hatch and develop to the infectious larval stage.

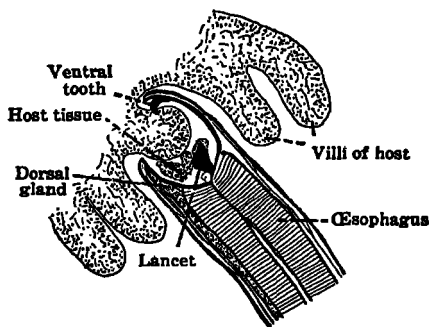


FIG. 183. — NEMATODA. Hookworm, *Ancylostoma*. Anterior end of adult attached to intestinal wall of man. Some of the tissue of the host is included in the buccal cavity of the worm. (After Loos, modified.)

*Ancylostoma braziliensis* is a parasite common in cats and dogs in various countries including the southern United States. Under favorable conditions the infective larvæ of this species may penetrate the skin of man through which it migrates parallel to the surface forming a tortuous path and causing the condition known as creeping eruption. Ethyl acetate on cotton and carbon dioxide snow have been found to be effective methods of treatment. Another species of hookworm living in cats and dogs is *A. caninum*. It is cosmopolitan in distribution and very pathogenic to puppies.

The species in the family METASTRONGYLIDÆ are much less important. *Dictyocaulus filaria* is the thread lung worm of sheep, goats, cattle, etc. Its eggs hatch in the lungs and the larvæ migrate through the trachea into the alimentary canal from which they escape from the mouth in the saliva or from the anus in the fæces. The larvæ, which become infective in about ten days, crawl to the tip of blades of grass with which they may be ingested by herbivorous animals. They establish themselves in the lungs causing a catarrhal condition.

To the family TRICHOSTRONGYLIDÆ belong several interesting parasites of lower animals. *Hæmonchus contortus* is one of the commonest parasites of domestic sheep throughout the world, and also occurs in other ruminants. It lives principally attached to the wall of the fourth stomach. The eggs are deposited in the fæces of the host and the infective larvæ crawl to the tip of blades of grass where they may be ingested by grazing animals. The infection results in anæmia. *Heligmosomum muris* is a species of trichostrongyl parasitic in wild rats in the United States that may be obtained easily for study.

**Order FILARIOIDEA.** — The round worms in this order have become adapted to life in the blood, lymph, muscle, and connective tissue of vertebrates and require an insect intermediate host for their transmission. Representatives of three families are of particular interest, FILARIIDÆ, DRACUNCULIDÆ, and SPIRURIDÆ. *Wuchereria bancrofti* (Fig. 178, b) is a species of the FILARIIDÆ that lives in man and is widely spread in tropical countries. The larvæ of this species are about  $\frac{1}{100}$  inch long. During the daytime they live in the lungs and larger arteries, but at night they migrate to the blood vessels in the skin. Mosquitoes, which are active at night, suck up these larvæ with the blood of the infected person. The larvæ develop in the mosquito's body, becoming

about one twentieth of an inch long, make their way into the mouth parts of the insect, and enter the blood of the mosquito's next victim. From the blood they enter the lymphatics and may cause serious disturbances, probably by obstructing the lymph passages. This results in a disease called elephantiasis. The limbs or other regions of the body swell up to an enormous size, but there is very little pain. No successful treatment has yet been discovered, and the results are often fatal. Infection with this parasite is common in man especially in the West Indies, South America, and West and Central Africa. Many inhabitants of Charleston, S. C., are infected, the worms having been introduced probably by negro slaves from Africa.

Another interesting species of the family FILARIDÆ is the eye worm, *Loa loa* (Fig. 178, c), of West Africa. It migrates around the body through the subdermal connective tissue, sometimes across the eyeball. No severe pathological lesions are produced. The transmitting agents are mango flies of the genus *Chrysops*. Among other species in this family are *Onchocerca volvulus*, which occurs also in West Africa and produces subdermal nodular swellings; *Dirofilaria immitis*, which may be present in tangled masses in the right ventricle of the dog's heart; *Setaria equina*, a frequent parasite of the peritoneal cavity of horses and other EQUIDÆ; and species that are common in birds, especially crows and English sparrows, in whose blood large numbers of the microfilariae may be present.

*Dracunculus medinensis*, the guinea worm, belongs to the family DRACUNCULIDÆ. It is a common human parasite in tropical Africa, Arabia, and India, that has been known for centuries and is probably the "fiery serpent" mentioned by Moses (*Numbers*, XXI). The adult female, which may reach a length of over three feet, is located usually in the subcutaneous tissue of the arm, leg, and shoulders. The young larvæ are discharged from the worm and escape through an opening in the human skin; if they reach water and chance to encounter the fresh-water crustacean *Cyclops* they burrow into it and metamorphose in the body cavity. Man becomes infected by swallowing the *Cyclops* in drinking water. The method of extracting the worm that has been practiced for hundreds of years is to roll it up on a stick gradually, a few turns each day, until the entire worm has been drawn out.

Species of the family SPIRURIDÆ are mostly parasites of birds,

reptiles, and mammals. *Habronema megastoma* lives in the stomach of the horse and is prevalent in the southern United States. It produces nodules or tumors in the stomach and is transmitted by the house fly. *Adruenna strongylina* is a worm that forms tumors in the stomach wall of pigs in this country. *Gongylonema scutatum* (Fig. 178, *e*) inhabits the mucosa of the œsophagus of sheep, cattle, and goats. The intermediate hosts are dung beetles.

**Order Dioctophymoidea.** — The round worms in this order are parasites of the digestive tract, kidneys, and body cavity of birds and mammals and the larvæ develop in an intermediate host. *Dioctophyme renale* is the largest known nematode and may reach a length of over three feet. It is most frequently encountered in the kidney of the dog which is gradually consumed by the worm.

Renal colic and failure of the infected kidney to function are symptoms. Fish are thought to be the intermediate hosts.

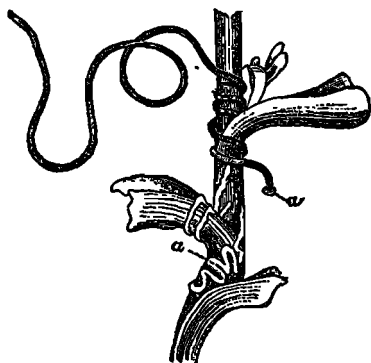
The family TRICHINELLIDÆ is the only one in the order TRICHINELLOIDEA. Two important human parasites, the trichina worm and whipworm, and several interesting parasites of rats belong here.

*Trichinella spiralis* (Fig. 184, 178 *d*, *f*) causes the disease of human beings, pigs, and rats called trichinosis. The parasites enter the human body when in-

FIG. 184. — *Gordius*, twining around a water plant and laying eggs. *a, a*, clump and string of eggs. (After von Linstow.)

adequately cooked meat from an infected pig is eaten. The larvæ soon become mature in the human intestine, and each mature worm deposits probably about 10,000 young. These young (Fig. 178, *d*) are either placed directly into the lymphatics by the female worms or burrow through the intestinal wall; they encyst in muscular tissue in various parts of the body (Fig. 184). As many as 15,000 encysted parasites have been counted in a single gram of muscle. Pigs acquire the disease by eating offal or infected rats. In a few countries pork is inspected for this and other parasites by government agents.

The whipworm, *Trichuris trichiura*, lives in the cecum and ap-



pendix of man. Its body is drawn out anteriorly into a long slender whip-like process (Fig. 178, *h*). There is no intermediate host. The eggs escape in the faeces and ripen outside of the body. Ripe eggs when swallowed hatch in the intestine and the larvæ become located in the cecum. Whipworms injure the host very little. *Hepaticola hepatica* occurs in the liver and *Trichosomoides crassicauda*

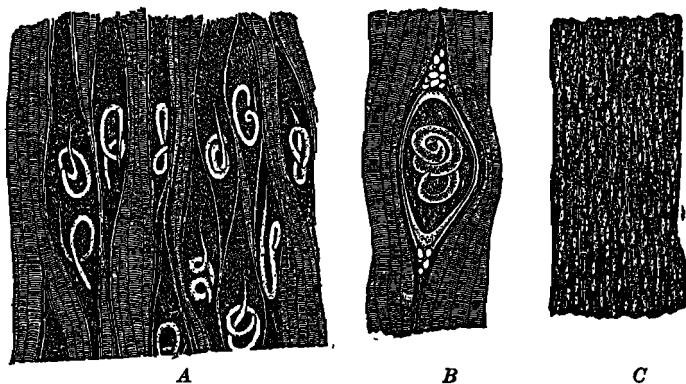


FIG. 185. — *Trichinella spiralis*. A, larvæ among muscle fibers, not yet encysted. B, a single larva encysted. C, piece of pork, natural size, containing many encysted worms. (After Leuckart.)

in the urinary bladder of rats. These species may be found of value as examples of round worms for laboratory study.

**Subclass GORDIACEA** — The worms in this subclass are usually referred to as horse-hair snakes (Fig. 185) and are erroneously supposed to arise from horse-hairs. Morphologically they differ widely from the EUNEMATODA. The body is opaque and no lateral lines are present; in both sexes the intestine and genital ducts open into a cloaca; spicules are absent in the male; the body cavity is lined with epithelium; the ova escape into the body cavity and thence into the oviducts; and the alimentary canal is atrophied in the sexually mature worms. The eggs are laid in the water in long strings where the adults live. The larvæ that hatch from the eggs penetrate into a young mayfly or some other aquatic insect; they escape in some unknown way from this host and find their way into a second host, usually a beetle, cricket, or grasshopper; in the body cavity of the second host the larvæ continue their development eventually passing out into the water where they become sexually mature. Since the adults live only in water, those

that survive probably emerge from terrestrial insects, which constitute their second intermediate hosts, that chance to become drowned in watering troughs and small pools frequently formed after a rain. *Gordius aquaticus* (Fig. 185) is a cosmopolitan species; *Paragordius varius* is common in North America; and *Nectonema agile* lives as a parasite in marine crustaceans at Woods Hole, Mass., and elsewhere.

## 2. CLASS II. ACANTHOCEPHALA

The spineheaded worms (Fig. 186) which belong to this class, live in the intestine of vertebrates attached to the wall by a protrusible proboscis usually covered with recurved hooks. They

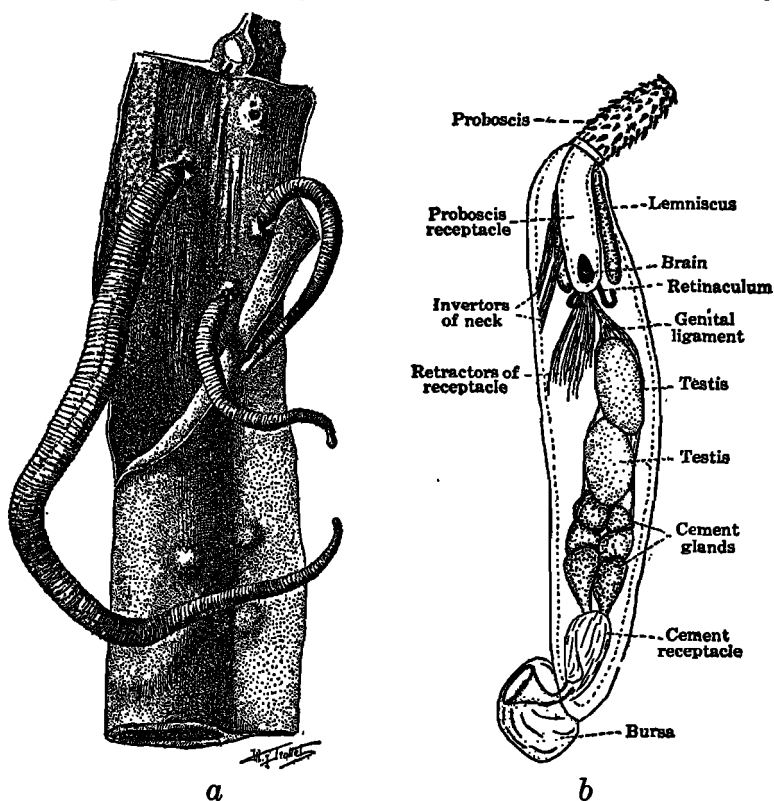


FIG. 186. — ACANTHOCEPHALA. a, *Gigantorhynchus gigas* clinging to the intestinal wall of a pig. The two small worms are males, and the larger is a female. b, A male specimen of the genus *Acanthocephalus* showing internal organs. (a, after Brumpt; b, after Van Cleave.)

vary in length from several millimeters to over 50 centimeters. No alimentary canal is present at any stage in their life cycle, food being absorbed through the surface of the body. The sexes are separate and reproductive systems are complex. The eggs break out into the body cavity of the female where they develop into embryos; they are then expelled from the body of the worm and pass out of the vertebrate host in the feces. An intermediate host is required for further development, either an insect or a crustacean. Among species that have been reported from the United States are *Neoechinorhynchus emydis* from turtles, *Echinorhynchus salvelini* from lake trout, *Arhynchmorhynchus brevis* from the bittern, *Macracanthorhynchus hirudinaceus* from pigs, and *Moniliformis moniliformis* from rats and mice. Several species, including the last two named above, have been reported from man.

### 3. NEMATHELMINTHES IN GENERAL

The descriptions presented in the preceding pages should give the student a good idea of the general features of the NEMA-



FIG. 187. — NEMATODA. The heads of two free-living species that show the complexity of structure of certain nemas. (After Cobb.)

THELMINTHES. One misconception that might arise, however, is that the unsegmented round worms are more simple than they are; their thread-like shape, smooth surface, and dull colors tend to obscure their real complexity. One of the foremost students



of the group (Cobb) has published a diagram of a free-living nematode containing 116 labels, and, in another place, illustrates how complicated their morphology may be, by figures showing the mouth parts of several species (Fig. 187).

The eggs of round worms are distinctive in size and shape and of importance in the identification of species, especially of those that live in man (Fig. 188). They may be discharged either before or during segmentation, or with the embryo fully developed. In a few species the embryos hatch within the uterus of the female worm and are then brought forth viviparously. The embryonic development is simple and much alike in all species. The larvæ upon hatching have the main characteristics of nematodes but are not sexually developed. Many parasitic species have certain adaptive larval characters which are subsequently lost. In the course of its development, the worm undergoes about four moults with the adult stage following after the fourth or last moult. Among the parasitic species some of these moults may take place within the egg before hatching, during its free existence, while within the tissue of an intermediate host, or within the tissues of the definitive host.

**The germ track in animals.** — The classical example of the germ track in animals is that of *Ascaris megalocephala*. The first cleavage division of the egg results in two daughter cells, each containing two long chromosomes (Fig. 189, A). In the second division the chromosomes of one cell divide normally and each daughter cell receives one half of each (B). The chromosomes of the other cell behave differently; the thin middle portion of each breaks up into granules (A) which split, half going to each daughter cell, but the swollen ends (B) are cast off into the cytoplasm. In the 4-cell stage there are consequently two cells with the full amount of chromatin and two with a reduced amount. This inequality in the amount of chromatin results in different-sized nuclei (C); those with entire chromosomes are larger than those that have lost the swollen ends. In the third division one of the two cells with the two entire chromosomes loses the swollen ends of each; the other (D) retains its chromosomes intact. A similar reduction in the amount of chromatin takes place in the fourth and fifth divisions and then ceases. The single cell in the 32-cell stage which contains the full amount of chromatin has a larger nucleus than the other thirty-one cells and gives rise to all of the germ cells, whereas the

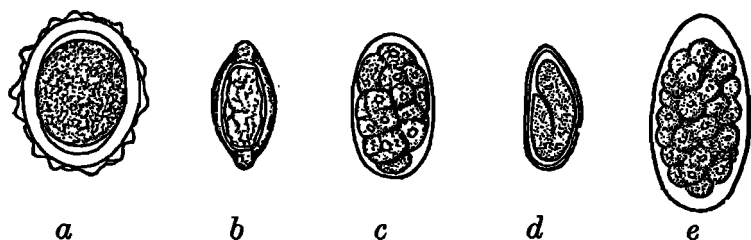


FIG. 188. — NEMATODA. Eggs of species that live in man. (After Cort.)  
a, *Ascaris lumbricoides*. b, *Trichuris trichiura*. c, *Ancylostoma duodenale*.  
d, *Enterobius vermicularis*. e, *Trichostrongylus orientalis*.

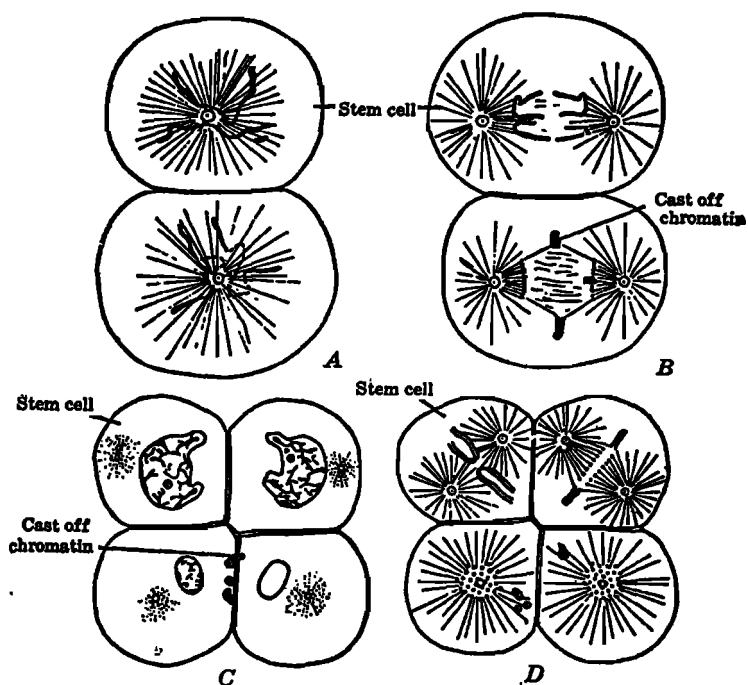


FIG. 189. — The germ track in *Ascaris*. Stages in early cleavage showing the chromatin-diminution process in all cells except the stem cell. (From Boveri.)

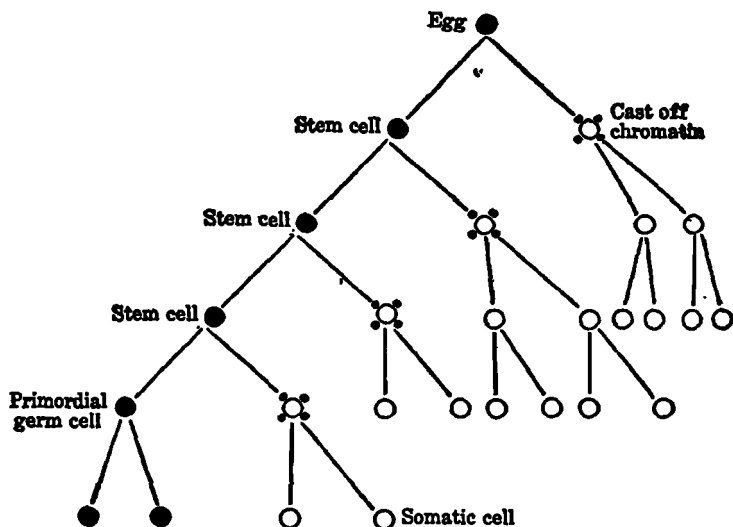


FIG. 190. — *Ascaris*. Diagram showing segregation of the primordial germ cell. (From Boveri.)

other cells are for the production of somatic cells only. The cell lineage of *Ascaris* is shown in the accompanying diagram (Fig. 190).

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## CHAPTER VII

### ROTIFERA, GASTROTRICHA, BRYOZOA, BRACHIOPODA, CHÆTOGNATHA, AND PHORONIDEA

The groups of animals considered in this chapter are all comparatively few in numbers and somewhat difficult to classify. Some of them are recognized as distinct phyla by certain zoologists. By others the ROTIFERA and GASTROTRICHA are united to form the phylum TROCHELMINTHES; the BRYOZOA, BRACHIOPODA, and PHORONIDEA to form the phylum MOLLUSCOIDEA; and the CHÆTOGNATHA and ANNELIDA to form the phylum CœLHELMINTHES. It seems best at this time to treat them separately and leave their final position in the animal kingdom for zoologists to determine on the basis of more satisfactory data than are available at present.

#### 1. ROTIFERA

The ROTIFERA, or ROTATORIA, (Fig. 191), commonly known as wheel animalcules, are extremely small METAZOA. They were at one time considered INFUSORIA. Most of them are inhabitants of fresh water, but some are marine and a few parasitic. The anatomy of a ROTIFER is shown in figure 191. The *head* is provided with *cilia* which aid in locomotion and draw food into the mouth. The *tail* or *foot* is bifurcated and adheres to objects by means of a secretion from a *cement gland*. The body is usually cylindrical and is covered by a shell-like *cuticle*.

The PROTOZOA and other minute organisms used as *food* are swept by the cilia through the *mouth* into the *pharynx*, also called the *mastax* or chewing stomach. Here chitinous *jaws*, which are constantly at work, break up the food. The movements of these jaws easily distinguish a living rotifer from other organisms. The food is *digested* in the glandular *stomach*. Undigested particles pass through the *intestine* into the *cloaca* and out of the *anus*.

Two coiled tubes, which give off a number of ciliated lobules, and enter a bladder, constitute the *excretory system*. The bladder contracts at intervals, forcing the contents out of the anus. Since the amount of fluid expelled by the bladder is very large, it is probable

that *respiration* is also a function of this organ, the oxygen being taken into the animal with the water which diffuses through the

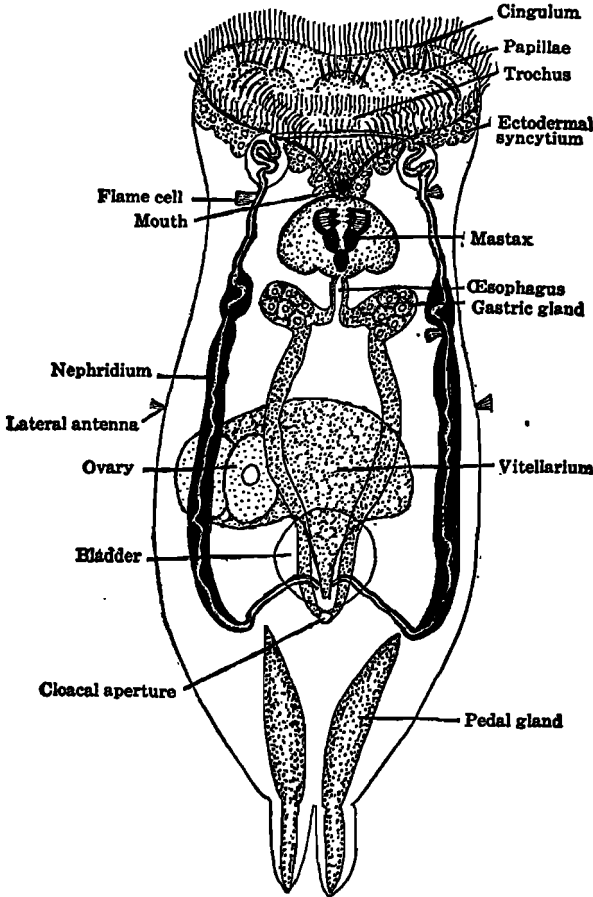


FIG. 191. — ROTIFERA. *Hydatina senta*. Female, ventral view. (After Borradaile and Potts, modified.)

body wall, and the carbonic acid being cast out with the excretory fluid. The body cavity is not a true coelom.

The *sexes* of rotifers are separate. The *female* possesses an *ovary* in which the eggs arise, a *yolk gland* which supplies the eggs with yolk, and an *oviduct* which carries the eggs into the cloaca. From here the eggs reach the exterior through the anus. The *males* are usually smaller than the females, and often degenerate. They

possess a *testis* in which the spermatozoa arise, and a *penis* for transferring the spermatozoa to the female.

Two kinds of eggs are produced by rotifers: (1) summer eggs, and (2) winter eggs. The *summer eggs*, which develop partheno-

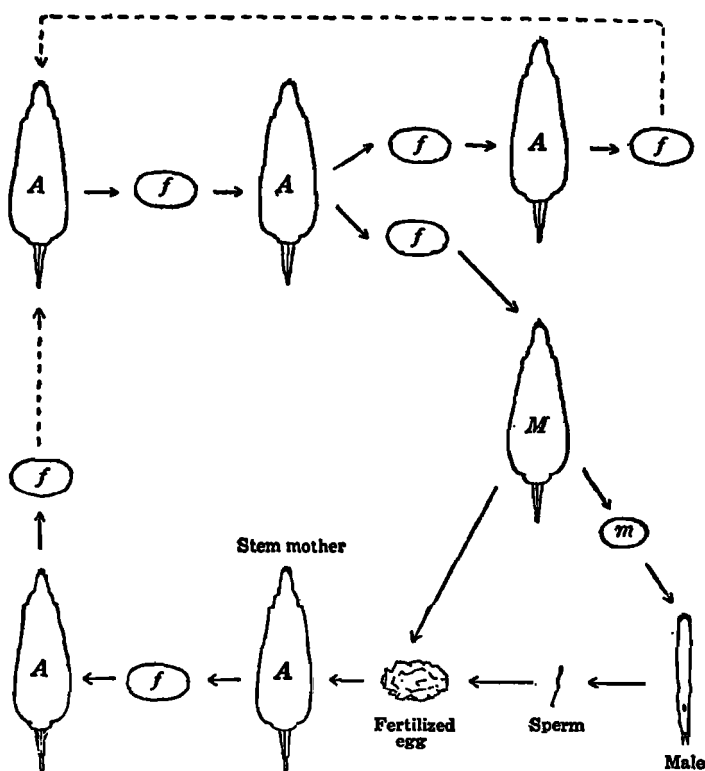


FIG. 192. — Diagram showing the alternation of generations in a rotifer, such as *Lecane inermis*. The most common type of individual, the "amictic" female (A), reproduces exclusively by diploid parthenogenesis. Its eggs (f) develop invariably into females, which are usually amictic, so that multiplication by diploid parthenogenesis may continue for many generations (as indicated by the long, broken-lined arrows). But the daughters of the amictic female may be "mictic" (M). Their eggs are haploid, and develop parthenogenetically (m) into males, or, if fertilized, produce amictic females, the "stem mothers," with which the cycle begins anew. (After Miller.)

genetically, are thin-shelled, and of two sizes; the larger produce females and the smaller males. The *winter eggs*, which are fertilized, have thick shells, and develop females. Figure 192 shows by means

of diagrams the alternation of generations in a rotifer, such as *Lecane inermis*.

One peculiarity of the rotifers worth mentioning is their *power to resist desiccation*. Certain species, if dried slowly, secrete gelatinous envelopes which prevent further drying; in this condition they live through seasons of drought, and may be subjected to extremes of temperature without perishing.

The resemblances between rotifers and the trochophore larvæ of certain mollusks, annelids, and other animals to be described later, is quite striking. The larva of the NEMERTINEA (*Pilidium*, Fig. 168) is likewise similar in some respects to an adult rotifer. This has led to the theory that the rotifers are animals somewhat closely related to the ancestors of the mollusks, annelids, and certain other groups.

**Classification of Rotifers.** — Rotifers are microscopic in size, triploblastic, and unsegmented. They possess a mastax (Fig. 193, *m, n, o*) in the pharynx, frequently a crown of cilia (corona) at the anterior end, and usually a foot or jointed tail at the posterior end. If we consider the ROTIFERA a phylum, we may recognize two classes and five orders as follows (Fig. 193).

**CLASS I. MONOGONATA.** — These have one ovary. They do not creep like a leech. They include most of the species frequently encountered.

**Order 1. NOTOMMATIDA.** — Free-swimming or creeping species with the mouth not in the center of the corona. The simplest of all rotifers belong to the genus *Proales* (Fig. 193, *a*). They are small and cylindrical, with short foot and toes, and without a tail; the corona is a uniformly ciliated area and does not possess portions bearing longer cilia, called auricles. *Proales sordida* is a representative species. The genus *Nommata* contains species with auricles and elongated body, usually a tail and small foot and toes; there are many species which live among water plants. *N. truncata* is red in color, truncate at each end, and has a very small foot. *Furcularia forficula* has the cuticula somewhat stiffened and conspicuous toes, but no auricles. Certain species of the genus *Furcularia* (Fig. 193, *b*) spring about wildly, aided by powerful strokes of the foot and toes. *Salpina spingera* (Fig. 193, *c*) has the cuticula hardened into a lorica of three or four plates from which project teeth or spines. *Diurella tigris* also possesses a lorica, and two long, bristle-like toes; it is very common among aquatic vegetation. *Trochosphaera*



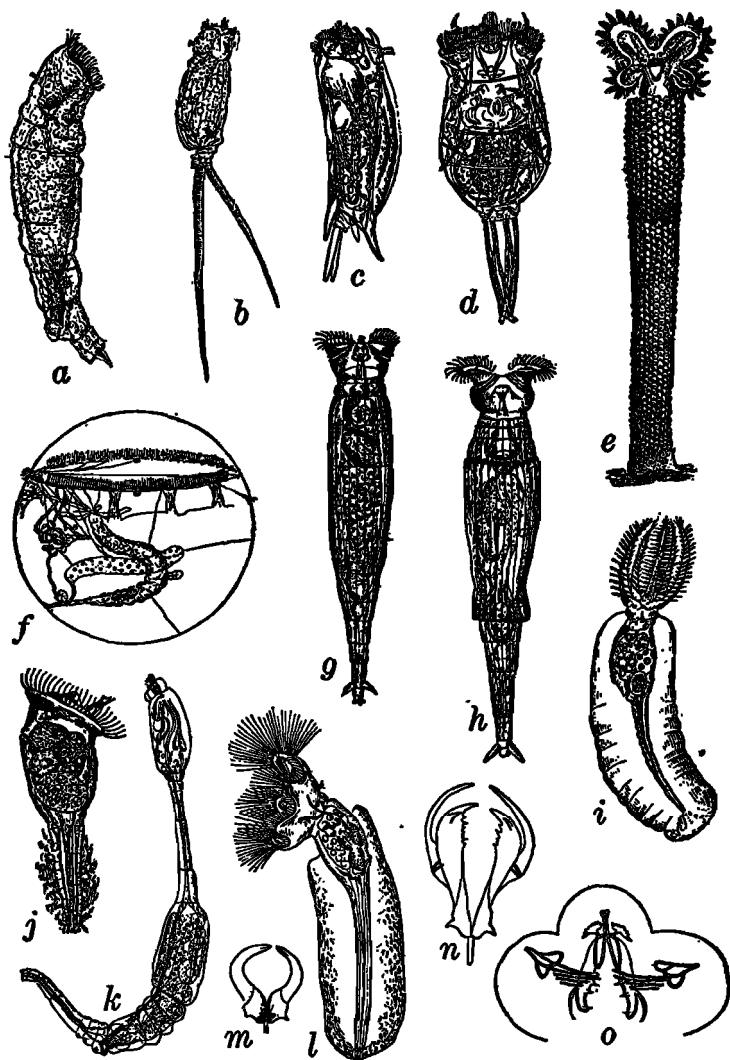


FIG. 193. — Types of Rotifers and their jaws. (From Jennings, after various authors.) a, Order NOTOMMATIDA, *Proales werneckii*. b, Order NOTOMMATIDA, *Furcularia longiseta*. c, Order NOTOMMATIDA, *Salpina spinigera*. d, Order NOTOMMATIDA, *Brachionus pala*. e, Order MELICERTIDA, *Melicerta ringens*. f, Order NOTOMMATIDA, *Trochosphaera solstitialis*. g, Order BDELLOIDA, *Rotifer citrinus*. h, Order BDELLOIDA, *Philodina roseola*. i, Order FLOSCULARIDÆ, *Stephanoceros eichhornii*. j, Order MELICERTIDA, *Conochilus unicornis*. k, Order SEASONIDA, *Seison annulatus*. l, Order FLOSCULARIDÆ, *Floscularia proboscidea*. m, Jaws of *Asplanchnopus myrmeleo*. n, Jaws of *Asplanchna priodonta*. o, Jaws of *Harringia eupoda*.

*solstitialis* (Fig. 193, *f*) is an interesting species because of its resemblance to the free-swimming trochophore larvæ of annelids, nemertines, etc.

*Hydatina senta* (Fig. 191) is a large, well-known rotifer 0.5 mm. long that has been used extensively by zoologists for experimental work in genetics. It has a corona on which the cilia are arranged in the form of a wreath; inside of this are three prominences bearing bristles which serve as sense organs. In *Brachionus rubens* (Fig. 193, *d*) these three prominences are represented by longer projections, and the cuticle forms a lorica with six anterior spines. *Asplanchna herricki* is a large species, sac-like in form, and without foot or anus, waste products being cast out through the mouth. It thrusts its forceps-like jaws out of the mouth and seizes other animals with them. The plankton of the Great Lakes sometimes contains enormous members of this and related species.

**Order 2. FLOSCULARIDÆ.** — The adult males and young rotifers belonging to this order are free-swimming but the adult females are mostly solitary and attached to water plants by a stalk which is the modified foot. They live in a transparent tube and usually possess a lobed corona that is much expanded, and has the mouth in the center. The cilia at the edge of the corona are often long and do not beat actively but are moved about so as to entangle prey. In these forms the digestive tract is modified for dealing with the large animals captured by the corona. *Floscularia ornata* (Fig. 193, *l*) has a corona with five knobbed lobes, a foot about twice as long as the body but no eyes. *Stephanoceros fimbriatus* (Fig. 193, *i*) also has a corona with five lobes; these are very long and slender and their cilia are long and non-vibratile.

**Order 3. MELICERTIDA.** — In this order the rotifers have a large corona with two parallel rows of cilia around the outer edge, the inner row being larger than the outer. Between these two rows is usually a groove, often lined with fine cilia, along which food particles are carried to the mouth. The jaws are of the peculiar malleo-ramate type. The species may be solitary or colonial, free-swimming or attached. *Melicerta ringens* (Fig. 193, *e*) has a large corona with four large lobes, lives in a tube formed of spherical pellets and is common on water plants. *Conochilus unicornis* (Fig. 193, *j*) is a free-swimming, pelagic species, living in small colonies in which each individual occupies a separate, transparent tube.

**CLASS II. DIGONONTA.** — These have two ovaries and creep like a leech.

**Order 1. BDELLOIDA.** — Fresh-water species that swim with the corona or creep or both. Behind the corona is a dorsal proboscis. The body is usually cylindrical and without a lorica; it is composed of rings that may be drawn together like the sections of a telescope. *Rotifer vulgaris* (Fig. 193, *g*) is a common species about 0.5 mm. long. The corona bears two wheels of cilia on separate retractile lobes. The body is whitish and opaque; the foot is long and has three toes; and the proboscis is provided with two eyes. *Philodina roseola* (Fig. 193, *h*) often occurs in infusions. It has two eyes behind the proboscis and a slender, rose-colored body. *Callidina* and certain other genera are able to withstand dessication and come to life when placed in water, after existing for months in a dried condition.

**Order 2. SEISONIA.** — These rotifers are parasitic on marine crustacea. The corona is greatly reduced; the body is long, narrow, and ringed; the neck is much elongated; and the elongated foot has a terminal perforated disk with which it attaches itself to its host. Two genera belonging to this order are *Seison* (Fig. 193, *k*) and *Paraseison*.

**Constancy in the number of tissue cells or nuclei.** — The cells of which various organs are constituted, do not vary greatly in size within the individuals of a species hence variations in the size of the body or of an organ are generally considered to be due to differences in the number of cells. In many animals, however, it has been shown that certain organs are almost invariably made up of a definite and constant number of cells or nuclei and in some animals the cell or nuclear number of the entire somatic tissue is constant. This has been demonstrated with the greatest completeness in the rotifer, *Hydatina senta* (Fig. 191). In this species each individual possesses 958 somatic nuclei distributed as shown on page 285.

In the differentiated somatic cells of such an animal the power of mitotic cell division appears to be lost; for example, no regeneration occurs in the rotifer, *Stephanoceros* (Fig. 193, *i*), if its arms are injured.

Cell or nuclear constancy occurs in species in which there is determinate cleavage of the egg. Apparently partial constancy is more frequent than complete constancy. In four genera belonging to the family NEOECHINORHYNCHIDÆ of the ACANTHOCEPHALA,

THE NUCLEI OF *Hydatina senta*

I. Skin and associated structures	
subcuticular cells of body and tail.....	108 nuclei
foot glands.....	19
2 bipolar cells.....	2
cingulum.....	46
trochus.....	19
mouth.....	43
between trochus and cingulum...	28
bipolar cells of crown.....	36
	<hr/>
	301
II. Pharynx	
75 epithelial cells with.....	91
38 muscle cells with.....	42
nerve cells.....	22
ganglion and doubtful cells.....	12
	<hr/>
137 cells with.....	167
III. Digestive tract	
oesophagus.....	15
stomach.....	35
gastric glands.....	12
intestine.....	14
	<hr/>
	76
IV. Urinogenital system.....	43
V. Musculature.....	120
VI. Nervous system.....	247
VII. Retrocerebral organ.....	4
	<hr/>
Total for all somatic tissues....	958 nuclei

however, all of the somatic tissues have a constant number of cells although the number may differ in different species. The nematode worm, *Oxyuris curvula*, has a constant number of cells (412) in the excretory and nervous systems and in the connective tissue, but a variable number in other organs. The number of muscle cells in the body wall of 7 different species belonging to the genus *Oxyuris* is the same for all, namely 65. Similarly the cells in the ommatidia of the compound eye of arthropods are not only constant in number but also constant in their location and physiological interrelations. Cell or nuclear constancy may occur also among the germ cells. For example, in the fly, *Miastor* (see Index), a definite number of primordial germ cells, and later, of ova, develop in each individual. Many other instances of cell or nuclear constancy are

known among the tunicates, insects, annelids, nematodes, turbellarians, trematodes, etc.

## 2. GASTROTRICHA

To this group belong a number of microscopic animals that live in fresh water and are often abundant among algæ and débris upon which they feed. They may reach a length of about 0.5 mm. They resemble rotifers somewhat and are sometimes included with rotifers

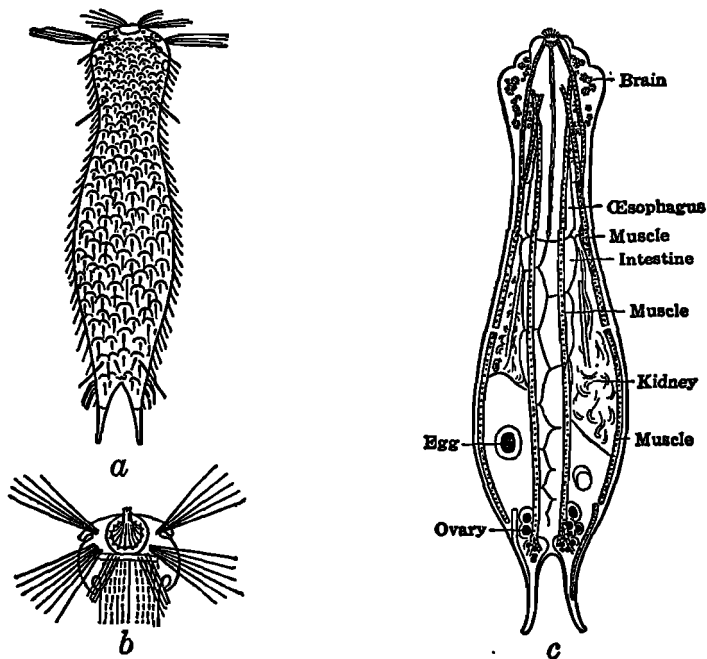


FIG. 194. — GASTROTRICHA. a, *Chætonotus larus*: dorsal view. b, *Lepidoderma rhomboides*: ventral view of head. c, *Chætonotus maximus*, showing internal organs. (a, c, after Zebrika; b, after Stokes.)

fers in a phylum called TROCHELMINTHES. They have also been considered relatives of the nematode worms. The general shape and structure is shown in Fig. 194. The animal is indistinctly divided into *head*, *neck*, and *body*. There is a *mouth* at the anterior end surrounded by *oral bristles*, groups of *sensory bristles* on the sides of the head, and often a forked *tail* containing *cement glands* used to fasten the animal to solid objects. Locomotion is accomplished by bands of *cilia* and resembles that of INFUSORIA, or by

long bristles with which the animals jump about like certain rotifers.

The *intestine* is a straight tube leading to an *anus* near the posterior end of the body. The *muscular system* consists of six pairs of delicate longitudinal strands. In the head are the nerve cells that constitute the *brain* from which fibers lead to the sides of the head and posterior end of the body. In some species pigmented *eye spots* are present. The *excretory organs* are represented by a pair of coiled tubes with a flame cell at the inner end of each and two pores opening near the middle of the ventral surface. Only females have been described; these may really be hermaphroditic but no male gonads have thus far been discovered. The *eggs* are very large, sometimes about one half the length of the body; they are attached to filamentous algæ or other solid objects and each gives rise to a fully developed organism.

Over 30 species of GASTROTRICHA have been described, 17 or more from North America. *Chaetonotus latus* (Fig. 194, *a*) is a common species with a short, unsegmented, forked tail and short, conical spines covering the dorsal surface. It is 0.12 mm. long. *Lepidoderma rhomboides* (Fig. 194, *b*) has a deeply forked tail consisting of 20 segments, scales covering the back, and a deep, transverse depression back of the mouth. It is 0.3 mm. long. *Ichthydium podura* resembles CHÆTONOTUS but the back is bare except for a pair of vertical spines on the neck and another near the posterior end.

### 3. BRYOZOA

The BRYOZOA, or POLYZOA, PHORONIDEA, and BRACHIOPODA are sometimes placed together under one phylum, the MOLLUSCOIDEA. It seems probable, however, that they not only represent distinct, but widely divergent groups, and should therefore be discussed separately.

The BRYOZOA, or *moss-animals*, are mostly *colonial*. They resemble hydroids, like *Obelia* (Fig. 111), in form, but differ from them markedly in structure. The majority of them live in the sea, but a few inhabit fresh water. *Bugula* is a common marine genus which shows the principal characteristics of the group.

The soft parts constituting the *polypide* lie within the true *cælotomic cavity* bounded by the body wall or *zoæcium*. The *mouth* lies in the midst of a crown of *ciliated tentacles* (Fig. 195, *a*) called the

*lophophore*, which serve to draw food particles into the body. The U-shaped *alimentary canal* consists of a ciliated *œsophagus*, a *stomach*, and an *intestine* which opens by means of an anus lying just outside the lophophore. One *retractor muscle* serves to draw the polypide into the zoecium. The *funiculus* is a strand of mesodermal tissue attached to the base of the stomach. There are no circulatory nor excretory organs.

Both an *ovary* and a *testis* are present in each individual; they may be found attached to the funiculus or the body wall. The eggs are probably fertilized in the coelom and then develop in a modified portion of the zoecium called the *oœcium*. The larvæ of some BRYOZOA resemble a trochophore (see p. 281).

Certain members of *Bugula* colonies are modified into structures

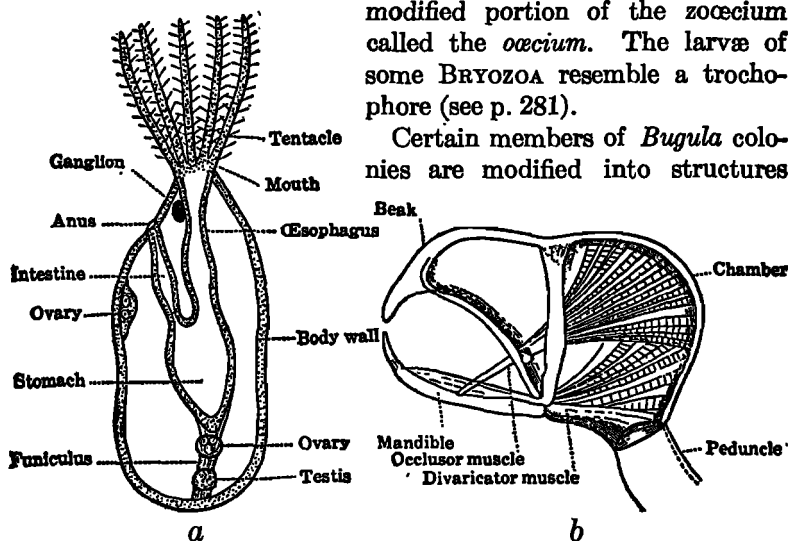


FIG. 195. — BRYOZOA. a, Diagram showing the structure of single individual. b, An avicularium of *Bugula*. (After Hincks.)

called *avicularia* (Fig. 195, b). These have jaws which probably protect the colony from the attacks of small organisms and prevent the larvæ of other animals from settling upon it.

Two classes of BRYOZOA are usually recognized, the ENDOPROCTA and ECTOPROCTA, although they differ from each other in certain respects so greatly that they may eventually be regarded as two separate phyla.

**CLASS I. ENDOPROCTA.** — This class includes a small number of fresh-water and marine species that appear to be primitive. There is no body cavity, the space between the body wall and intestine

being filled with parenchyma; the anus is located inside of the lophophore; a pair of nephridia ending in flame cells are present; the gonads have a special duct leading to a genital pore; and the lophophore bears a single row of tentacles which can be retracted into the depression in this structure called the vestibule. Some species are dioecious and others hermaphroditic. *Loxosoma davenporti* is a solitary species that bears buds; it is about 2 mm. long; has from 22 to 26 tentacles; and possesses a mammary organ in the vestibule to which developing embryos are attached. It is a marine species abundant in Vineyard Sound. *Pedicellina cernua* is a colonial, marine species the zooids of which arise from a creeping, branching stolon. It attaches itself to shells and algæ in shallow water along the Atlantic coast of the United States and Europe. *Urnatella gracilis* (Fig. 196, c) is a colonial species that lives on the underside of stones in running fresh water in the eastern and central states. Its zooids which are few in number, arise from a common disk and form long stalks which are jointed and form branches.

**CLASS II. ECTOPROCTA.** — This class includes fresh-water and marine species that possess a coelomic body cavity, an anus opening outside of the lophophore, no definite excretory organs, and a lophophore that can be retracted into the zoecium. Both unisexual and hermaphroditic species occur. Asexual reproduction by budding is common to all and large branching and encrusting colonies are formed by this means. Most of the BRYOZOA belong to this class.

**Order 1. PHYLACTOLEMATA.** — These are fresh-water species that have an oval or horseshoe-shaped lophophore, a sort of lip, called the epistome, projecting over the mouth and statoblasts usually provided with marginal air cells which float them on the surface of the water. *Plumatella princeps* (Fig. 196, a) forms a much-branched, creeping or erect colony and produces elongated statoblasts. *Cristatella mucedo* (Fig. 196, d) forms an elongate, creeping gelatinous colony, with zooids on the upper surface, and produces circular statoblasts with two rows of marginal hooks (Fig. 196, e). These statoblasts are buds with a hard chitinous shell that arise from the funiculus and give rise to new colonies after the death of the parent or a period of drought. *Pectinatella magnifica* (Fig. 196, b) forms rosette-shaped groups of associated colonies which may build up a thick gelatinous base. It has from 60 to 84 tentacles, and black, circular statoblasts with one row of



from 10 to 22 marginal hooks. *Fredericella sultana* forms a colony of intertwining branches. It has a lophophore that is oval, and produces dark brown, elliptical statoblasts without a float.

**Order 2. GYMNOLEMATA.** — These are mostly marine species that have a circular lophophore without an epistome. The mouth can usually be closed by a flap called the operculum and whip-like appendages (vibracula), avicularia and oecia are often present.

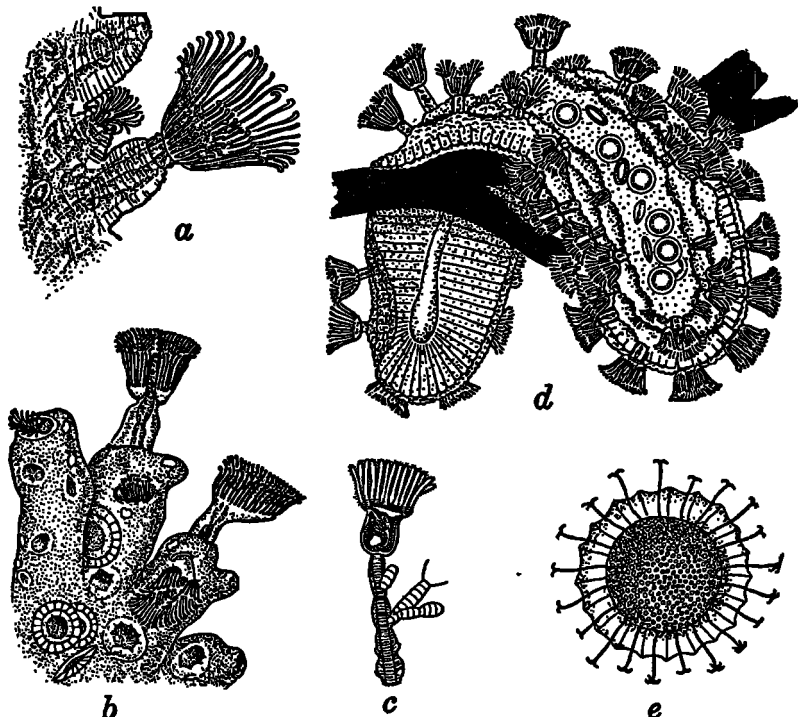


FIG. 196. — BRYOZOA. a, *Plumatella punctata*. b, *Pectinatella magnifica*. c, *Urnatella gracilis*. d, *Cristatella mucedo*. e, *C. mucedo*, statoblast. (a, b, after Kræpelin; c, after Leidy; d, e, after Allman.)

*Bugula* belongs to this order. *Crisia eburnea* (Fig. 197, a) has tubular zoecia, but lacks an operculum, avicularia, and vibracula. It forms branching, calcareous colonies that are white, and form bushy tufts. *Membranipora pilosa* (Fig. 197, b) is a common species near Woods Hole. It forms, usually, encrusting, calcareous colonies, each zooid having a thickened margin with 4 to 12 spines and below this a long or short corneous spine. *Alcyonidium hir-*

*sutum* forms yellowish-brown or reddish colonies that are often encrusting, with conical projections on the surface between which are the orifices. The zoecium is fleshy or membranous and its

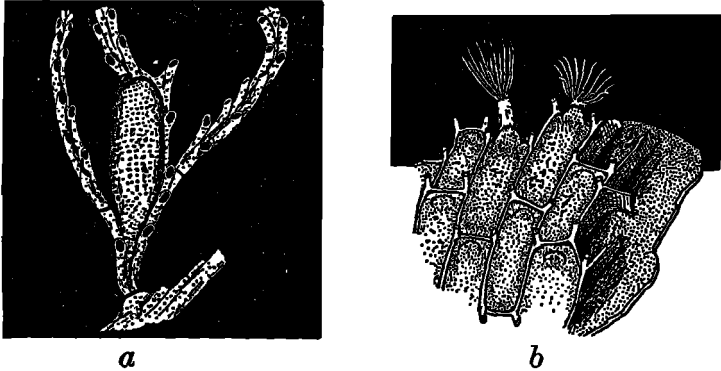


FIG. 197. — BRYOZOA. Order GYMNOLEMATATA. a, *Crisia maxima*: zoecium and ovicell. b, *Membranipora membranacea*. (From Johnson and Snook.)

aperture is closed by a folded membrane when the lophophore is retracted.

#### 4. BRACHIOPODA

The BRACHIOPODA are marine animals living within a calcareous bivalve *shell* (Fig. 199). They are usually attached to some object

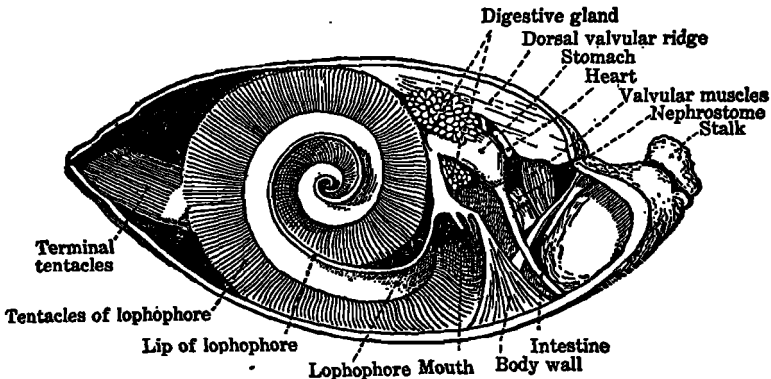


FIG. 198. — BRACHIOPODA. Longitudinal section of *Waldheimia*. (After Lister, from Shipley and MacBride.)

by a stalk, called the *peduncle* (Fig. 198). Because of their shell they were for a long time regarded as mollusks. The valves of

the shell, however, are dorsal and ventral instead of lateral as in the bivalve mollusks. Within the shell (Fig. 198) is a conspicuous structure called the *lophophore*, which consists of

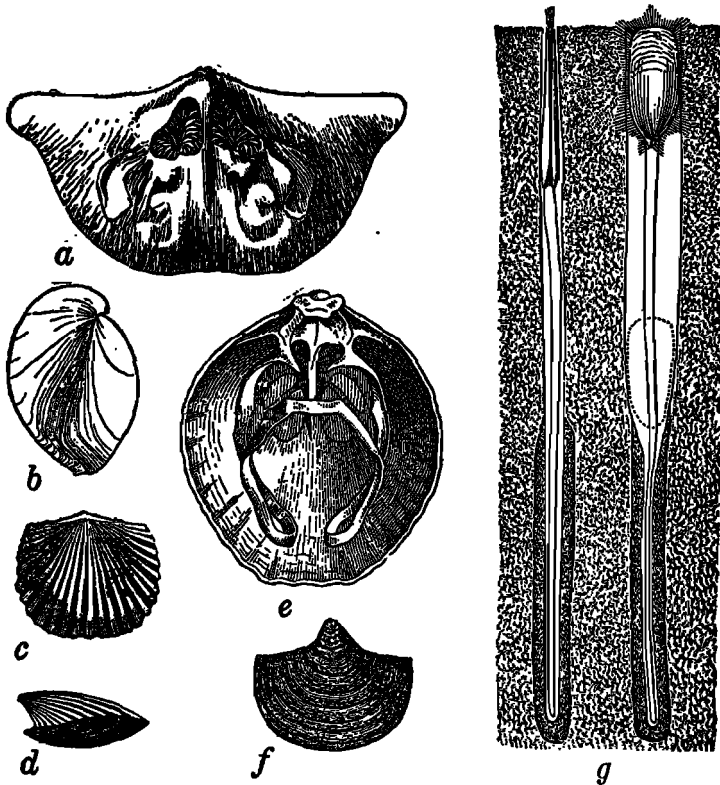


FIG. 199. — BRACHIOPODA. a, *Productus giganteus*: Carboniferous limestone; interior of dorsal valve. b, *Terebratulina semiglobosa*: upper Chalk; lateral view. c, d, *Orthis calligramma*: Ordovician. e, *Waldheimia*: interior of dorsal valve showing brachial skeleton. f, *Micromitra labradorica*: Lower Cambrian; ventral valve. g, *Lingula anatifera* in their tubes in the sand; the dotted line in the right tube indicates the position of the body when retracted. (a-f, from Woods, after various authors; g, after Francois.)

two coiled ridges, called arms; these bear ciliated tentacles. Food is drawn into the *mouth* by the lophophore. A true *cœlom* is present, within which lie the *stomach*, *digestive gland*, and the *heart*.

The group BRACHIOPODA is extremely old, and, although found

in all seas to-day, brachiopods were formerly more numerous in species and of much greater variety in form than at present. Some of them, for example *Lingula* (Fig. 199, *g*), are apparently the same to-day as they were in the Silurian period estimated at about twenty-five million years ago.

Two orders of brachiopods may be recognized according to whether or not the valves of the shell are joined together by a hinge.

**Order 1. ECARDINES.** — These have a shell without a hinge. There is an alimentary canal with an anus. No internal skeleton is present. Three families with about 32 living and 400 fossil species mostly paleozoic, belong to this order. *Lingula* (Fig. 199, *g*) has already been mentioned. *Glottidia albida* occurs on our Pacific coast from low water to a depth of 60 fathoms. It has a smooth, narrow shell about 30 mm. long and white in color, and a stout peduncle about 45 mm. long. *Crania anomala* lives at a depth of about 100 fathoms in the West Indies. The shell is about 18 mm. long and 22 mm. broad and brownish in color and is fastened by the ventral valve to a rock. No peduncle is present.

**Order 2. TESTICARDINES.** — These have a shell with a hinge and an internal skeleton. No anus is present. The three families in this order contain about 80 living and 2200 fossil species. *Terebratulina septentrionalis* has a thin, semi-transparent shell that is broadly oval in shape and yellowish or whitish in color. *Waldheimia floridana* has a shell that is triangular in shape and gray or brownish-white in color.

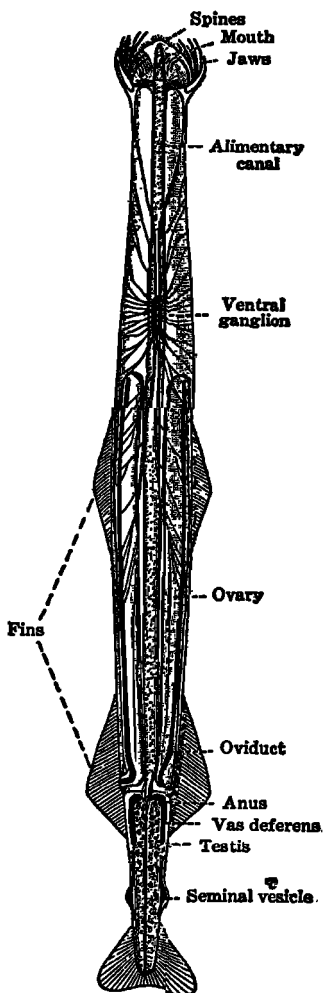


FIG. 200. — CHETOGNATHA: *Sagitta hexaptera*: ventral view; (After O. Hertwig, modified.)

## 5. CHÆTOGNATHA

The CHÆTOGNATHA are marine animals which swim about near the surface of the sea. The best-known genus is *Sagitta*, the arrow-

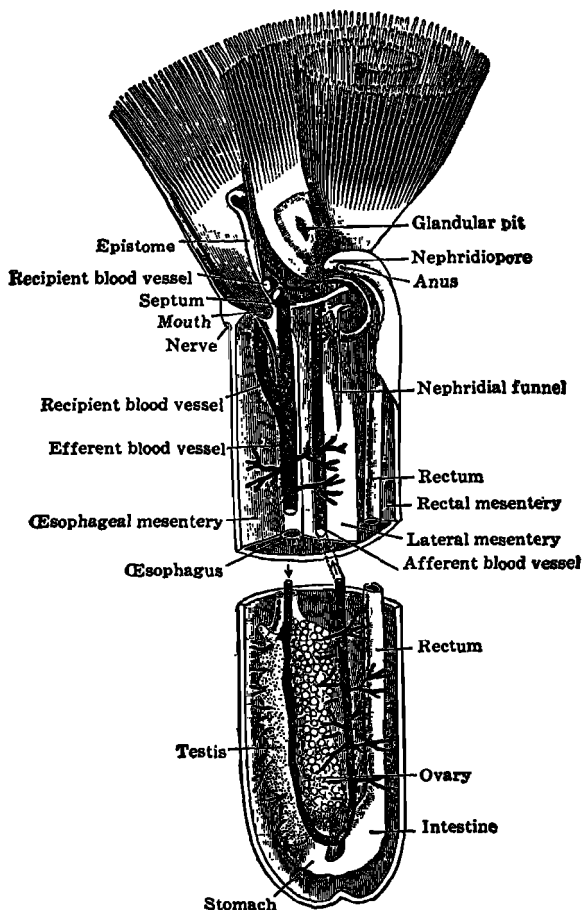


FIG. 201. — PHORONIDEA. *Phoronis*: diagram to show the structure.  
(From Benham.)

worm. Figure 200 shows most of the anatomical features of *Sagitta hexaptera*. The body consists of three regions, head, trunk, and tail. Lateral and caudal fins are present. There is a distinct coelom, an alimentary canal with mouth, intestine, and anus, a well-

developed nervous system, two eyes, and other sensory organs. The mouth has a lobe on either side provided with bristles which are used in capturing the minute animals and plants that serve as food. The members of the group are hermaphroditic.

*Sagitta bipunctata* is a pelagic species capable of vertical migration through many fathoms. *Eukrohnia hamata* has a slender body with a single lateral fin on either side. *Pterosagitta draco* has a broad body with a single pair of lateral fins and an integumentary expansion along the sides. All these species are cosmopolitan in their distribution.

## 6. PHORONIDEA

Most of the species in this group, about a dozen in all, belong to the genus *Phoronis* (Fig. 201). They are small, marine animals of sedentary habit that live in tubes. The larva, called an actinotrocha, is free-swimming and resembles a trochosphere. The adults are unsegmented, coelomate, and hermaphroditic. They possess a horse-shoe-shaped lophophore, an epistome, two excretory organs, and a vascular system. *Phoronis architecta* occurs in sand flats near the low-water mark in North Carolina. It lives in a straight tube about 13 cm. long and 1 mm. broad; is flesh colored; and has about 100 tentacles. *P. pacifica* is about 9 cm. long and 2 mm. broad, has about 190 tentacles, and lives on the Pacific coast of North America.

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## CHAPTER VIII

### PHYLUM ANNELIDA

#### INTRODUCTION

Annelids differ from the other groups of "worms" in the following respects: (1) the body is divided into a linear series of similar segments (also called metameres or somites) visible externally because of grooves that encircle the body, and internally because of partitions called septa; (2) the body cavity between the alimentary canal and body wall is a true coelom; (3) there is a single preoral segment, the prostomium; (4) the nervous system consists of a pair of dorsal preoral ganglia, the brain, and a pair of ventral nerve cords with typically a pair of ganglia in each segment; (5) typically a non-chitinous cuticle on the surface of the body supplied with chitinous bristles or setæ.

Five classes may be recognized in the phylum as follows:

**CLASS I. CHÆTOPODA.** — Marine, fresh-water, or terrestrial annelids with conspicuous segments, intersegmental septa, setæ, and a large coelom.

**Order 1. POLYCHÆTA.** — Marine CHÆTOPODA with many setæ situated on fleshy lateral outgrowths, the parapodia; usually a well-developed head bearing appendages; sexes separate; and a free-swimming trochophore larva. Ex. *Nereis virens*, *Amphitrite ornata*, *Arenicola cristata*.

**Order 2. OLIGOCHÆTA.** — Mostly terrestrial and fresh-water CHÆTOPODA with few setæ; no parapodia; no distinct head with appendages; hermaphroditic; no trochophore larva. Ex. *Lumbricus terrestris*, *Tubifex tubifex*.

**CLASS II. ARCHIANNELIDA.** — Small marine annelids without setæ or parapodia. Ex. *Polygordius appendiculatus*.

**CLASS III. HIRUDINEA.** — Leeches. Annelids usually dorso-ventrally flattened, with a prostomium and 32 body segments; two suckers, one surrounding the mouth and the other at the posterior end; no setæ nor parapodia; hermaphroditic; coelom small because of growth of mesenchyme cells. Ex. *Hirudo medicinalis*, *Macrobdella decora*.



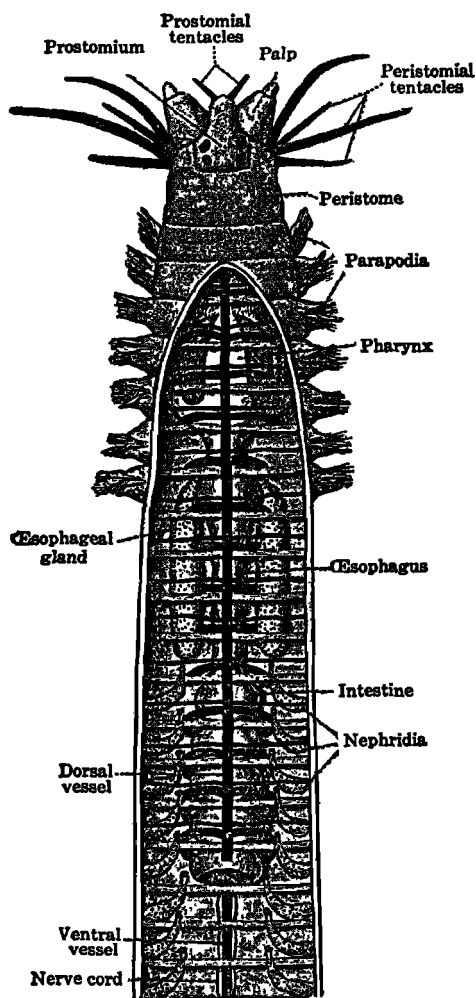


FIG. 202. — *Nereis*, the clamworm. Anterior end of the body with dorsal body wall removed. (After Parker and Haswell, modified.)

extends its body in search of food, or may leave the burrow entirely.

**External features.** — The body is flattened dorso-ventrally and may reach a length of over a foot. The *head* is distinct (Figs. 202, 203). Above the mouth is the *prostomium* which bears a pair of terminal *tentacles*, two pairs of simple *eyes*, and, on either side,

#### CLASS IV. GEPHYREA.

— Annelids without segmentation, setæ and parapodia; coelom large; trochophore larva. Ex. *Phascolosoma gouldi*.

#### CLASS V. MYZOSTOMARIA.

— Annelids parasitic on echinoderms; with five pairs of parapodia armed with acicula and hooks, usually ten pairs of cirri and normally four pairs of suckers. Ex. *Myzostoma cubanum*.

### 1. CLASS I. CHÆTOPODA

#### (1) NEREIS VIRENS — A CLAMWORM

The clamworm, *Nereis virens*, is a common annelid living in burrows in the sand or mud of the seashore at tide level. The burrows are sometimes two feet deep and are kept from collapsing by a lining of mucus which holds together the grains of sand. By day the clamworm rests in its burrow, but at night it

a thick *palp*. The first segment is the *peristomium*; from each side of this arise four tentacles or *cirri*. The crustaceans and other small animals that serve as food are captured by a pair of strong chitinous *jaws* which are everted with part of the pharynx when *Nereis* is feeding. Behind the head are a variable number of segments each bearing a fleshy outgrowth on either side, the *parapodia* (Fig. 203). These are used as locomotor organs, in addition to undulations of the body that are effective in swimming. New segments are added

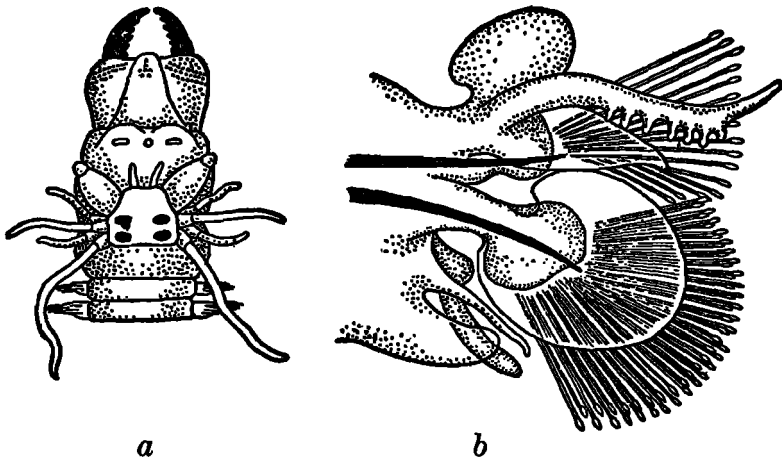


FIG. 203. — *Nereis*, the clamworm. a, Head with jaws and pharynx protruded in the position assumed when grasping food. b, A parapodium showing two acicula (in black), many locomotor setae and several flattened respiratory gills. (From Newman, after Leuckart.)

near the posterior end; here and near the anterior end the parapodia are not as well developed as elsewhere. The peristomium and posterior terminal segment are free from parapodia. Each parapodium consists of a dorsal blade, the *notopodium*, and a ventral blade, the *neuropodium*. The notopodium has a thin, vascular, dorsal lobe respiratory in function, and bears a dorsal *cirrus* and a bundle of long *setae*, one of which, the *aciculum*, is entirely internal, very thick, and attached to muscles within the body. The neuropodium also bears a cirrus and a similar bundle of *setae* with an *aciculum*. The posterior terminal segment bears a pair of ventral *cirri* that extend posteriorly, and the *anus*.

**Body wall** (Fig. 204). — This consists of an outer *cuticle*, which is secreted by the cells of the *hypodermis* just beneath it, and several

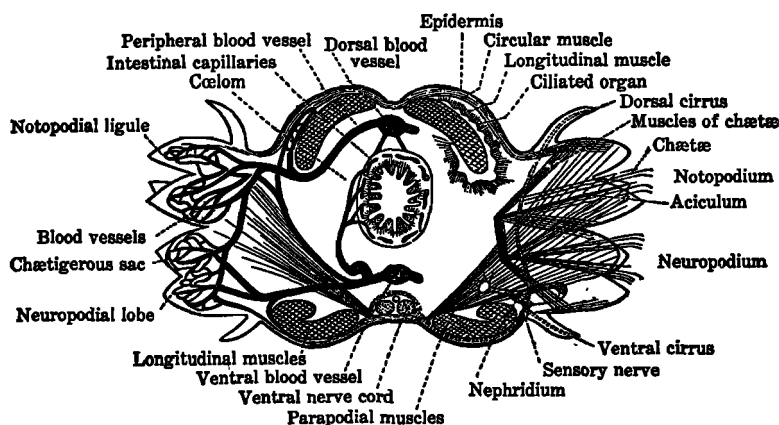


FIG. 204. — *Nereis*. Diagrammatic transverse section through the body. On the left the chief constituents of the vascular system are represented; on the right side the setæ (chaetæ) and their muscles, as well as the distribution of the lateral nerve, etc., are shown. (From Benham.)

*muscular layers* under the hypodermis. The first are circular muscles; then come two dorsal and two ventral bands of longitudinal muscles; and also a layer of oblique muscles. These muscles are covered within by a layer of *peritoneal epithelium*.

**Cœlom.**—The body cavity between the body wall and the intestine is a cœlom (Fig. 204). It is divided into chambers by transverse *septa* which correspond to the limits of the segments. Perforations in the septa beneath the intestine allow

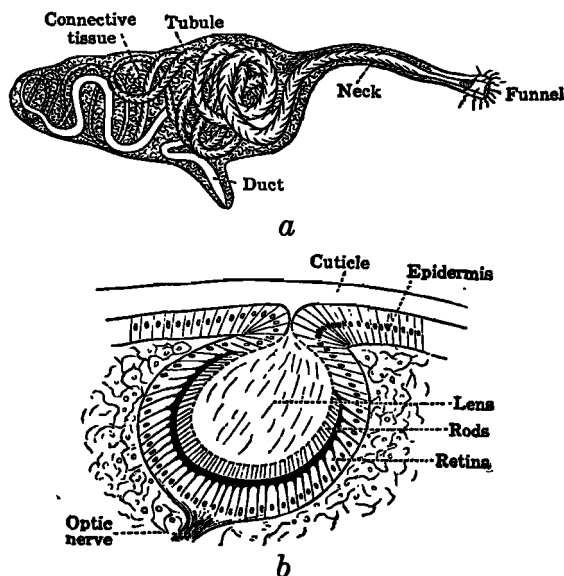


FIG. 205. — *Nereis*. a, Nephridium. b, Eye. (a, after Goodrich; b, after Andrews.)

fluid to pass from one chamber to the next. The coelom is lined with peritoneal epithelium.

**Digestive system** (Fig. 202).—The *mouth* opens into the *pharynx* which forms a sort of *proboscis* when protruded (Fig. 203, *a*). This is accomplished by protractor and retractor muscles. The pharynx leads into a slender *oesophagus* which has a *digestive gland* on either side opening into it. Following the oesophagus is a straight *stomach-intestine* extending to the anus.

**Circulatory system** (Fig. 202).—The blood is contained in contractile tubes, the blood vessels. There is a *dorsal vessel*, that lies between the two dorsal longitudinal muscle bands, which carries blood anteriorly, and a *ventral vessel* beneath the intestine which carries blood posteriorly. In each segment the two longitudinal vessels are connected on either side by right and left transverse vessels. From these arise two dorsal and two ventral branchial vessels that form networks of capillaries in the dorsal and ventral lobes of the parapodia.

**Excretory system.**—Every segment except the peristomium and the anal segment contains a pair of *nephridia* (Figs. 202, 205, *a*). Each nephridium opens into the coelomic cavity by means of a *ciliated funnel*; passes posteriorly through the septum into the following segment, where it forms a coiled tube; and opens at the base of a parapodium on the ventral surface through a *nephridiopore*. The parapodia serve as respiratory organs.

**Nervous system** (Fig. 206).—Above the pharynx in the head is a pair of supra-oesophageal ganglia that constitute the *brain*.

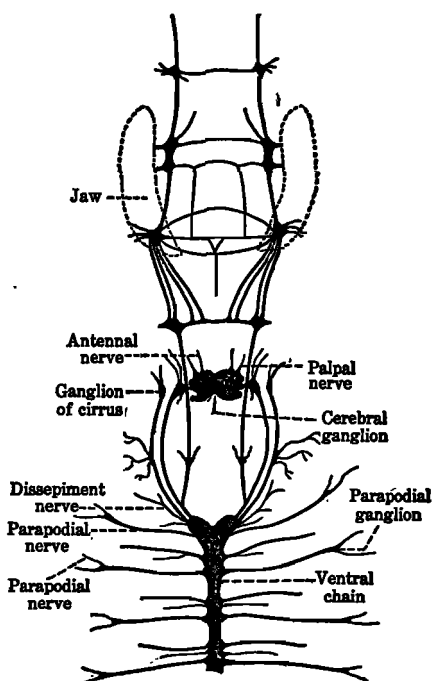


FIG. 206. — *Nereis*. Nervous system. (After Turnbull, from Petrunkevitch.)

This is connected with a pair of *subœsophageal ganglia* by a commissure on either side that form a ring around the pharynx. Following this is a *ventral nerve cord* with a pair of ganglia in each segment. The brain gives off an optic nerve to each eye, a palpal nerve to each palpus and a tentacular nerve to each group of tentacles. The peristomial tentacles receive nerves from small ganglia connected with the circumœsophageal commissure. Several dorsal and ventral ganglia around the pharynx, that are connected with one another and with the brain, constitute the *visceral nervous system*. From each of the ganglia of the ventral nerve chain arise three pairs of nerves, one pair to the parapodia, one to the anterior segment, and one to the muscles of the septum.

**Reproductive system.** — The sexes are separate. No well-defined *gonads* are present, but during the breeding season ova or spermatozoa arise from the wall of the cœlom in each segment except near the anterior end. They pass out through the nephridiopores and unite in fertilization in the open water. Trochophore larvæ develop from the fertilized eggs.

## (2) LUMBRICUS TERRESTRIS — AN EARTHWORM

The common earthworm, *Lumbricus terrestris*, or one of its near relatives, is usually used as a type in introductory courses in Zoology. Many beginning courses, however, omit this species hence a description of it is given here. It will serve to present the principal characteristics of the order OLIGOCHÆTA. Plate I presents in semi-diagrammatic form many of the anatomical features of the type.

**External features.** — The body of *Lumbricus* is cylindroid, and varies in length from about six inches to a foot. The *segments*, of which there are over one hundred, are easily determined externally because of the grooves extending around the body. At the anterior end a fleshy lobe, the *prostomium* (Fig. 212), projects over the *mouth*; this is not considered a true segment. It is customary to number the segments with Roman numerals, beginning at the anterior end, since both external and internal structures bear a constant relation to them. Segments XXXI or XXXII to XXXVII are swollen in mature worms, forming a saddle-shaped enlargement, the *clitellum*, of use during reproduction. Every segment except the first and last bears four pairs of *f*-shaped chitinous bristles, the *setæ* (Fig. 207); these may be moved by

retractor and protractor muscles, and are renewed if lost. The setæ on segment or *somite* XXVI are, in mature worms, modified for reproductive purposes.

The body is covered by a thin, transparent *cuticle* secreted by the cells lying just beneath it. The cuticle protects the body from physical and chemical injury; it contains numerous *pores* to allow the secretions from unicellular glands to pass through, and is marked with fine *striae*, causing the surface to appear iridescent (Fig. 208).

A number of *external openings* of various sizes allow the entrance of food into the body, and the exit of fæces, excretory products, reproductive cells, etc. (1) The *mouth* is a crescentric opening

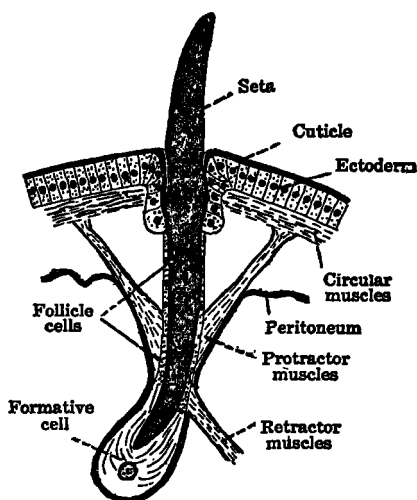


FIG. 207. — Earthworm, *Lumbricus*. Histology of seta and surrounding tissue. (After Stephenson, modified.)

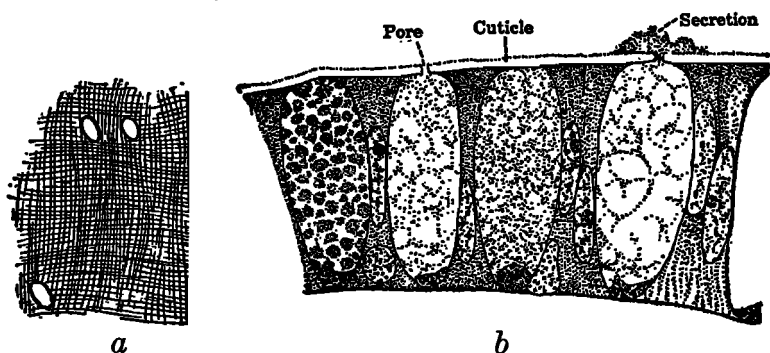


FIG. 208. — *Lumbricus*. a, Superficial view of the cuticle showing pores and striae. b, Vertical section of a bit of epidermis showing four mucus cells in different stages of secretion. Mucus is passing through one of the two pores in the cuticle. (From Dahlgren and Kepner.)

situated in the ventral half of the first somite (Fig. 212); it is overhung by the prostomium. (2) The oval *anal aperture* lies in the last somite. (3) The openings of the sperm ducts or *vasa deferentia* are situated one on either side of somite XV. They

have swollen lips; a slight ridge extends posteriorly from them to the clitellum. (4) The openings of the *oviducts* are small, round pores one on either side of somite XIV; eggs pass out of the body through them. (5) The openings of the *seminal receptacles* appear as two pairs of minute pores concealed within the grooves which separate somites IX and X, and X and XI. (6) A pair of *nephridiopores* (Fig. 209), the external apertures of the excretory organs, open on every somite except the first three and the last. They are usually situated immediately anterior to the outer seta of the inner

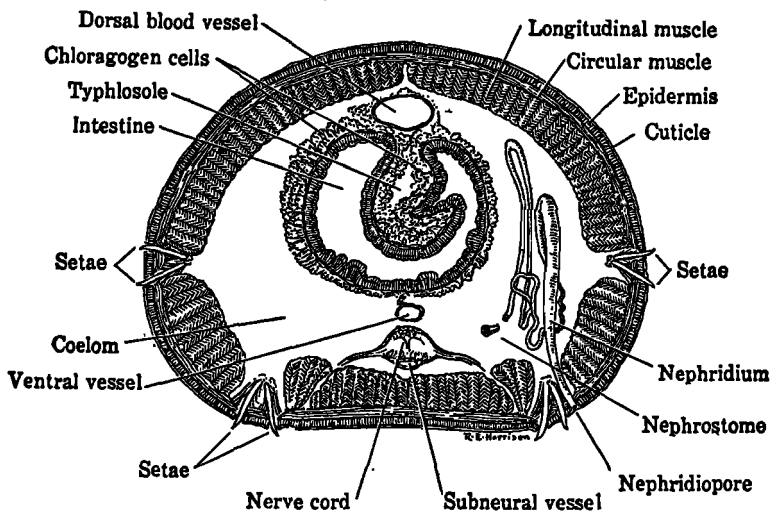


FIG. 209. — *Lumbricus*. Transverse section through the middle region of the body. (From Woodruff.)

pair. (7) The body cavity or *cœlom* communicates with the exterior by means of *dorsal pores*. One of these is located in the mid-dorsal line at the anterior edge of each somite from VIII or IX to the posterior end of the body.

**Internal anatomy** (Plate I). — If a specimen is cut open from the anterior to the posterior end by an incision passing through the body wall a trifle to one side of the mid-dorsal line, a general view of the internal structures may be obtained. The body is essentially a double tube (Fig. 209), the body wall constituting the outer, the straight alimentary canal, the inner; between the two is a cavity, the *cœlom*. The external segmentation corresponds to an internal division of the *cœlomic* cavity into compartments by means of partitions, called *septa*, which lie beneath the grooves.

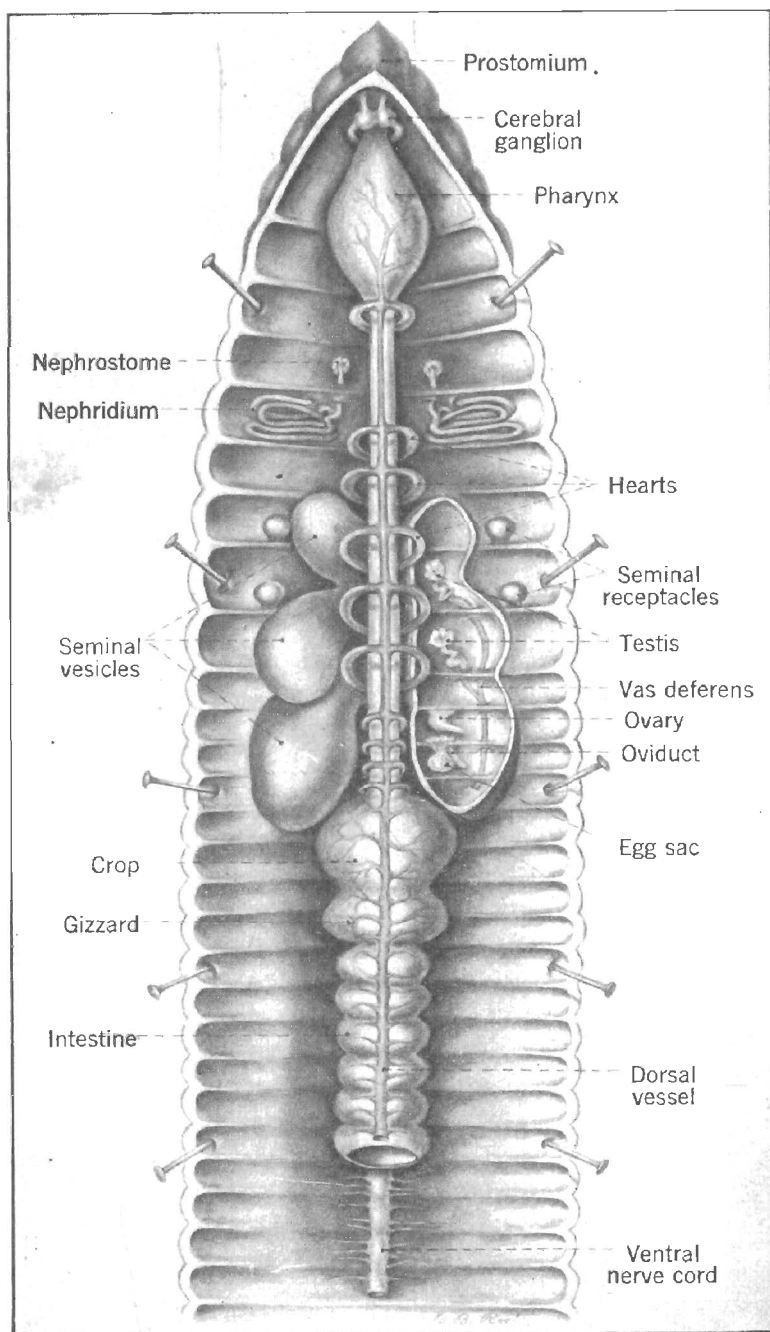


PLATE I. Anterior part of an Earthworm with dorsal body wall removed to show internal organs. The pins are inserted at intervals of five segments. (Drawn by Barbara Bradley Root.)



The alimentary canal passes through the center of the body, and is suspended in the coelom by the partitions. Septa are absent between somites I and II, and incomplete between somites III and IV, and XVII and XVIII. The walls of the coelom are lined with an epithelium, termed the *peritoneum*. The coelomic cavity is filled with a colorless fluid which flows from one compartment to another when the body of the worm contracts, thus producing a sort of circulation. In somites IX to XVI are the reproductive organs; running along the upper surface of the alimentary canal is the dorsal blood vessel; and just beneath it lie the ventral blood vessels and nerve cord.

**Digestive system.** — The *alimentary canal* (Plate I) consists of (1) a *mouth cavity* or *buccal pouch* in somites I to III, (2) a thick muscular *pharynx* lying in somites IV and V, (3) a narrow; straight tube, the *oesophagus* which extends through somites VI to XIV, (4) a thin-walled enlargement, the *crop* or *proventriculus*, in somites XV and XVI, (5) a thick muscular-walled *gizzard* in somites XVII and XVIII, and (6) a thin-walled *intestine* extending from somite XIX to the *anal aperture*. The intestine is not a simple cylindrical tube; but its dorsal wall is infolded, forming an internal longitudinal ridge, the *typhlosole* (Fig. 209). This increases the digestive surface. Surrounding the alimentary canal and dorsal blood vessel is a layer of *chloragogen cells*. The functions of these cells are not known with certainty, but they probably aid in the elaboration of food and are excretory. Three pairs of *calciferous glands* lie at the sides of the oesophagus in segments X to XII; they produce carbonate of lime, which probably neutralizes acid foods.

The *food* of the earthworm consists principally of pieces of leaves and other vegetation, particles of animal matter, and soil. This material is gathered at night. At this time the worms are active; they crawl out into the air, and, holding fast to the tops of their burrows with their tails, explore the neighborhood. Food particles are drawn into the buccal cavity by suction produced when the pharyngeal cavity is enlarged by the contraction of the muscles which extend from the pharynx to the body wall.

In the pharynx, the food receives a secretion from the pharyngeal glands; it then passes through the oesophagus to the crop, where it is stored temporarily. In the meantime the secretion from the calciferous glands in the oesophageal walls is added, neutraliz-

ing the acids. The gizzard is a grinding organ; in it the food is broken up into minute fragments by being squeezed and rolled about. Solid particles, such as grains of sand, which are frequently

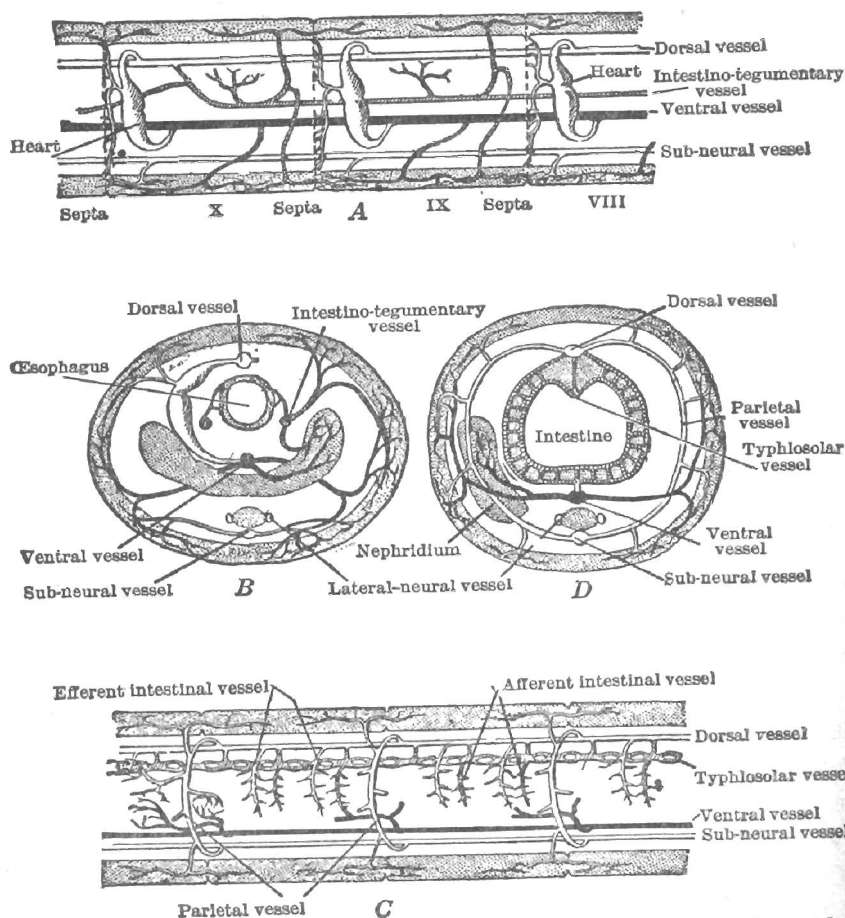


FIG. 210. — *Lumbricus*. Diagrams showing the arrangement of the blood-vessels. A, longitudinal view of the vessels in somites VIII, IX, and X. B, transverse section of same region. C, longitudinal view of the vessels in the intestinal region. D, transverse section through the intestinal region. (From Bourne, after Benham.)

swallowed, probably aid in this grinding process. The food then passes on to the intestine, where most of the digestion and absorption takes place.

**Circulatory system.** — The *blood* of the earthworm is contained in a complicated system of tubes which ramify to all parts of the body. A number of these tubes are large and centrally located; these give off branches which likewise branch, finally ending in

exceedingly thin tubules, the *capillaries*. The *blood* consists of a plasma in which are suspended a great number of colorless cells, called corpuscles. Its red color is due to a pigment termed *hæmoglobin* which is dissolved in the plasma. In vertebrates the hæmoglobin is located in the blood corpuscles.

There are *five longitudinal blood vessels* connected with one another and with various organs by branches, more or less regularly arranged. These are shown in figure 210, and are as follows:

(1) the dorsal or supra-intestinal vessel, (2) the ventral or subintestinal trunk, (3) the subneural trunk, (4) two lateral neural trunks, (5) five pairs of hearts in segments VII to XI, (6) two intestino-tegumentary vessels (in *A* and *B*) arising in segment X and extending to the oesophagus, integument, and nephridia in segments X to VI, (7) branches from the ventral trunk to the nephridia and body wall (*D*), (8) parietal vessels connecting the dorsal and subneural trunks in the intestinal region, (9) branches from the dorsal trunk to the intestine (in *C*), (10) a typhlosolar vessel connected by branches with the intestine and dorsal trunk, and (11) branches from the ventral vessel to the nephridia and body wall (in *D*).

The dorsal trunk (Fig. 211) and hearts determine the direction of the blood flow, since they furnish the power by means of their muscular walls. Blood is forced forward by wave-like contractions of the dorsal trunk, beginning at the posterior end and traveling quickly anteriorly. These contractions are said to be *peristaltic*, and have been likened to the action of the fingers in the operation of milking a cow. *Valves* in the walls of the dorsal trunk prevent the return of blood from the anterior end. In somites VII to XI the blood passes from the dorsal trunk into the hearts, and is forced by them both forward and backward in the ventral trunk. Valves

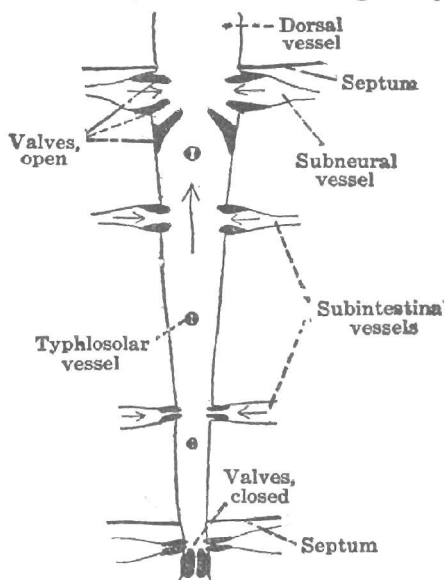


FIG. 211. — Earthworm, *Lumbricus*. Diagram of dorsal blood vessel to show connections and valves. (After Johnston.)

in the heart also prevent the backward flow. From the ventral trunk the blood passes to the body wall and nephridia. Blood is returned from the body wall to the lateral-neural trunks. The flow in the subneural trunk is toward the posterior end, then upward through the parietal vessels into the dorsal trunk. The anterior region receives blood from the dorsal and ventral trunks. The blood which is carried to the body wall and integument receives oxygen through the cuticle, and is then returned to the dorsal trunk by way of the subneural trunk and the intestinal connectives. Because of its proximity to the subneural trunk, the nervous system receives a continuous supply of the freshest blood.

The exchange of materials between the blood and the tissue cells takes place in minute *lymph spaces*. Blood plasma and a few corpuscles, which constitute the lymph, pass from the capillaries into these lymph spaces where the cells are bathed and the

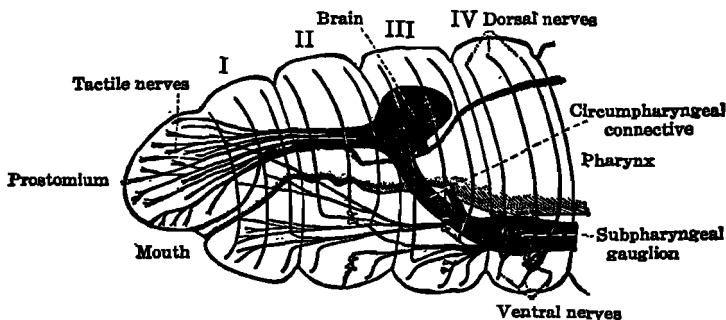


FIG. 212. — *Lumbricus*. Diagram of the anterior end to show the arrangement of the nervous system. (From Shipley and MacBride.)

interchange occurs. The lymph collects waste products of metabolism and makes its way back again into the blood stream.

**Respiration.** — The earthworm possesses no respiratory system, but obtains oxygen and gets rid of carbon dioxide through the moist outer membrane. Many capillaries lie just beneath the cuticle, making the exchange of gases easy. The oxygen is combined with the hæmoglobin.

**Excretory system.** — Most of the excretory matter is carried outside of the body by a number of coiled tubes, termed *nephridia* (Fig. 209), a pair of which are present in every somite except the first three and the last. A nephridium occupies part of two successive somites; in one is a ciliated funnel, the *nephrostome*, which

is connected by a thin ciliated tube with the major portion of the structure in the somite posterior to it. Three loops make up the coiled portion of the nephridium. The cilia on the nephrostome and in the nephridium create a current which draws solid waste particles from the coelomic fluid. Glands in the coiled tube take waste matter from the blood, and the current in the tube carries it out through the *nephridiopore*.

**Nervous system.**—The nervous system is concentrated. There is a bilobed mass of nervous tissue, the *brain* or *suprapharyngeal ganglion*, on the dorsal surface of the pharynx in segment III (Fig. 212). This is connected by two *circumpharyngeal connectives* with a pair of *subpharyngeal ganglia* which lie just beneath the pharynx. From the latter the *ventral nerve cord* (Fig. 209, Plate I) extends posteriorly near the ventral body wall. The ventral nerve cord enlarges into a ganglion in each segment and gives off three pairs of nerves in every segment posterior to IV. Each ganglion really consists of two ganglia fused together. Near the dorsal surface of every ganglionic mass are three longitudinal cords, the *neu-rochords* or "giant fibers" (Fig. 214). The brain and nerve cord constitute the *central nervous system*; the nerves which pass from and to them represent the *peripheral nervous system* (Fig. 213).

The nerves of the peripheral nervous system are either efferent or afferent. *Efferent* nerve fibers (Fig. 214) are extensions from cells in the ganglia of the central nervous system. They pass out to the muscles or other organs, and, since impulses sent along them give rise to movements, the cells of which they are a part are said to be *motor nerve cells*. The *afferent* fibers originate from nerve cells in the epidermis which are sensory in function, and extend

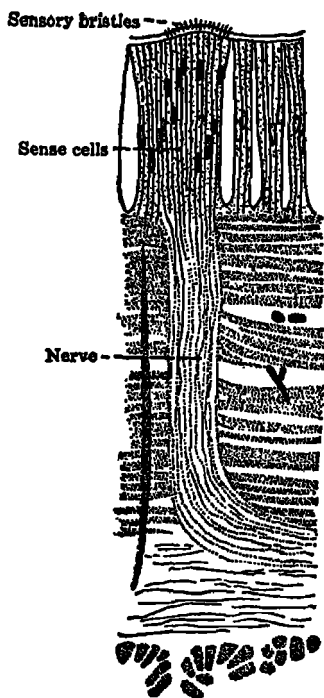


FIG. 213. — *Lumbricus*. Tactile nerve endings in the integument. (From Dahlgren and Kepner.)

into the ventral nerve cord. Recent experiments have shown that the peripheral nervous system is not a nerve-net, but is composed of elements which have definite connections in the nerve cord.

**Sense organs.** — The sensitiveness of *Lumbricus* to light and other stimuli is due to the presence of a great number of *epidermal sense organs*. These are groups of sense cells connected with the central nervous system by means of nerve fibers and com-

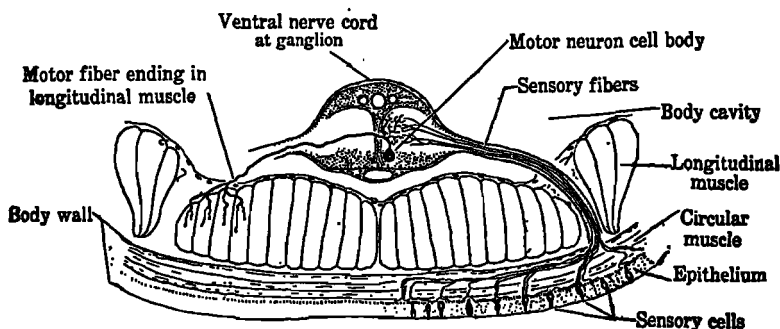


FIG. 214. — *Lumbricus*. Diagram of primary sensory and motor neurons of the ventral nerve cord, showing their connections with the skin and the muscles to form a simple reflex arc. (After Parker, from Woodruff.)

municating with the outside world through *sense hairs* which penetrate the cuticle. More of these sense organs occur at the anterior and posterior ends than in any other region of the body.

**Reproduction.** — Both male and female sexual organs occur in a single earthworm (Plate I). Figure 150 shows diagrammatically the position and shape of the various structures. The *female system* consists of: (1) a pair of *ovaries* in segment XIII; (2) a pair of *oviducts* which open by a ciliated funnel in segment XIII, enlarge into an *egg sac* in segment XIV, and then open to the exterior; and (3) two pairs of *seminal receptacles* or *spermathecae*, in somites IX and X. The *male organs* are (1) two pairs of glove-shaped *testes* in segments X and XI, (2) two *vasa deferentia* which lead from ciliated funnels to the exterior in segment XV, and (3) three pairs of *seminal vesicles* in segments IX, XI, and XII, and two central reservoirs.

Self-fertilization does not take place, but *spermatozoa* are transferred from one worm to another during a process called *copulation*. Two worms come together, as shown in figure 215, *a*; slime tubes

are formed, and then a band-like *cocoon* is secreted about the clitellar region. Eggs and spermatozoa are deposited in the cocoon, but fertilization does not occur until the cocoon is slipped over the head (Fig. 215, b).

The *eggs* of the earthworm are *holoblastic*, but cleavage is unequal. A hollow blastula is formed and a gastrula is produced by invagination. The mesoderm develops from two of the blastula cells, called *mesoblasts*. These cells divide, forming two *mesoblastic bands* which later become the epithelial lining of the coelom. The embryo

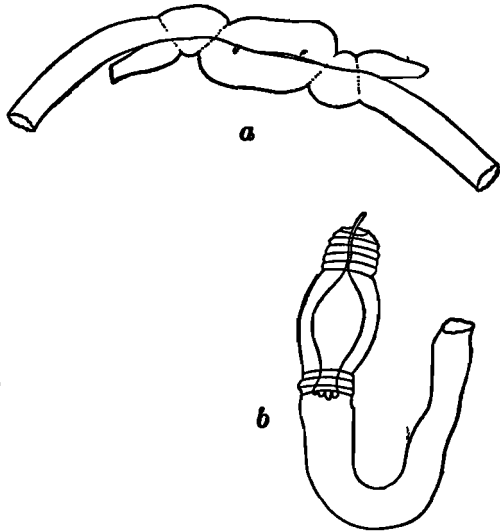


FIG. 215. — *Lumbricus*. a, the anterior segments of two copulating earthworms. Slime tubes encircle the pair from the 8th to the 33d segment. b, cocoon, freshly deposited, surrounded by one half of a slime tube. (After Foot.)

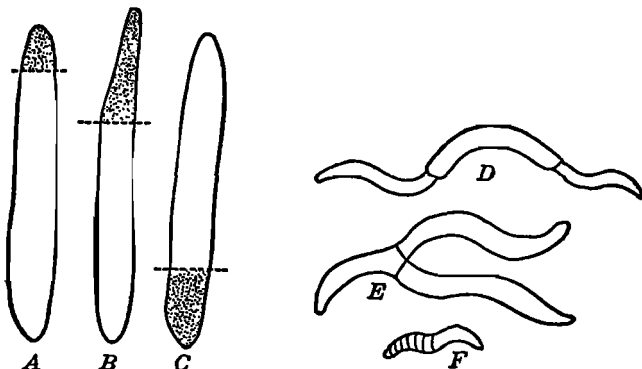


FIG. 216. — *Lumbricus*. A, head end of five segments regenerated from the posterior piece of a worm. B, tail regenerated from the posterior piece of a worm. C, tail regenerated from an anterior piece of a worm. D, union of three pieces to make a long worm. E, union of two pieces to make a double-tailed worm. F, anterior and posterior pieces united to make a short worm. The dotted portion represents regenerated material. (From Morgan.)

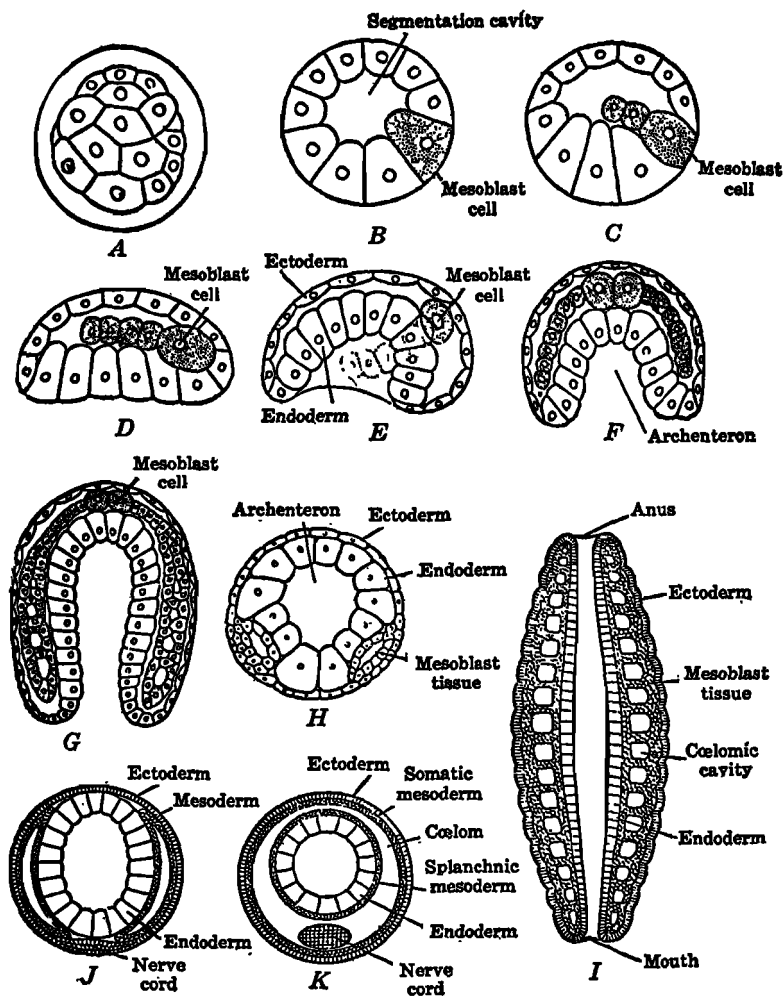


FIG. 217. — *Lumbricus*. Diagrams of stages in development. A, blastula (surrounded by a membrane); B, section of a blastula showing blastocoel and one of the primary cells (pole cells) of the mesoderm; C, later blastula with developing mesoderm bands; D, start of gastrulation; E, lateral view of gastrula showing invagination, which as it proceeds leaves the mesoderm bands on either side of the body as indicated by the cells represented with dotted outline; F, section of E, along the line, to show pole cells, mesoderm bands and enteric cavity; G, later stage showing cavities in the mesoderm bands; H, the same (G) in cross section; I, diagram of a longitudinal section of a young worm after formation of mouth and anus; J, the same in cross section; K, later stage in cross section. (From Woodruff, after Sedgwick and Wilson.)



escapes from the cocoon as a small worm in about two or three weeks. Stages in the development of an earthworm are shown and explained in figure 217.

**Regeneration and grafting.**—Earthworms have considerable powers of regeneration and grafting. Some of the results of experiments along this line are shown in figure 216. A posterior piece may regenerate a head of five segments (*A*) or in certain cases a tail (*B*). Such a double-tailed worm slowly starves to death. An anterior piece regenerates a tail (*C*). Three pieces from several worms may be united so as to make a long worm (*D*); two pieces may fuse, forming a worm with two tails (*E*); and an anterior piece may be united with a posterior piece to make a short worm (*F*). In all these experiments the parts were held together by threads until they became united.

### (3) OTHER CHÆTOPODA

The principal characteristics of the CHÆTOPODA are exhibited by *Nereis virens* and *Lumbricus terrestris*. Many variations from these types occur, some of which are noted below. The suborders and a few of the more important families and their commoner representatives are as follows.

**Order 1. POLYCHÆTA.**—Marine; parapodia with many setæ; usually well-developed head bearing appendages; sexes separate; and free-swimming, trochophore larva. The

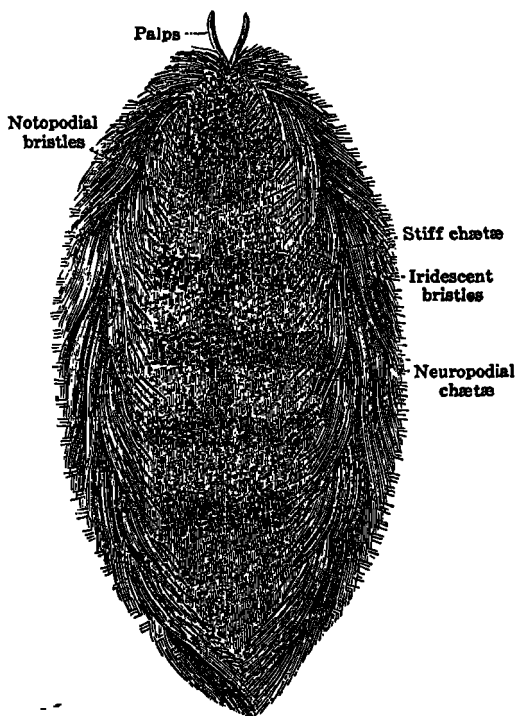


FIG. 218. — CHÆTOPODA. *Aphrodite aculeata*, the "sea-mouse." (From Benham, after Regne Animal.)

polychaetes may be divided into two suborders containing free-swimming and tube-dwelling species respectively.

**Suborder 1. ERRANTIA.** — Free-swimming; segments of body similar except at anterior and posterior ends.

**Family 1. APHRODITIDÆ** (Fig. 218). — These have the back partly or entirely covered with scales which usually alternate with slender cirri. *Lepidonotus squamatus* has 12 pairs of scales (elytra); is dark brown in color; about 3 cm. long; and lives under stones near the tide lines along the New England shore.

**Family 2. SYLLIDÆ.** — Short, slender worms usually with long slender dorsal cirri; asexual budding common. *Autolytus cornutus*

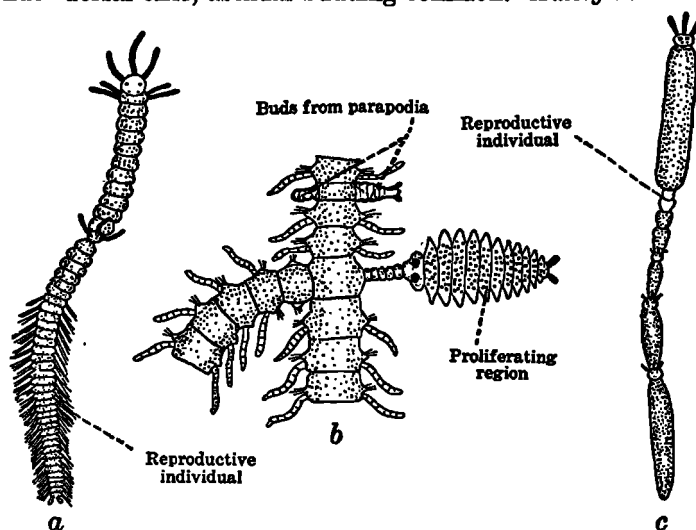


FIG. 219. — POLYCHÆTA. Asexual reproduction. a, *Syllis*, with the posterior region forming a reproductive individual. b, *Syllis*, showing branching of the asexual stock and budding of reproductive individuals from parapodia. c, *Autolytus*, with a chain of reproductive individuals budded off successively from a proliferating region. (After Borradaile and Potts, modified.)

(Fig. 219, c) is pinkish in color and about 15 mm. long. Asexual budding results in a linear row of offspring each of which acquires a head before separating from the parent.

**Family 3. NEREIDÆ.** — Ex. *Nereis virens*.

**Family 4. LEODICIDÆ.** — Slender worms of various lengths, with usually branching gills arising from the parapodia near the anterior end; proboscis with complicated jaw apparatus, and generally a parchment-like tube. *Leodice fucata* is known as

the palolo worm which lives in coral rock in the Gulf of Mexico and the West Indies. Swarming occurs in July within three days of the full moon.

**Suborder 2. SEDENTARIA.** — Tube-dwelling; head small or much modified; parapodia simple; branchiæ localized to a definite region.

**Family 1. CHÆTOPTERIDÆ.** — Long worms living in mud or sand in U-shaped parchment-like tubes; with body divided into three well-marked regions. *Chætopterus pergamentaceus* (Fig. 220) is 15 cm. long; has a stout body with a flattened anterior region; a middle region of five segments, four much swollen and the fifth with wing-like parapodia; highly phosphorescent.

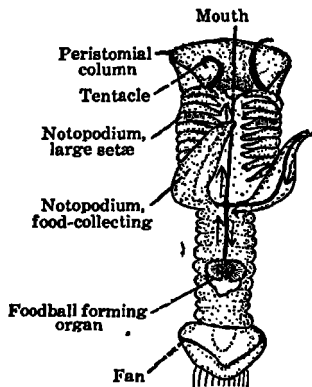


FIG. 220. — POLYCHÆTA. *Chætopterus*. Dorsal view of anterior end. Arrows show direction of the water currents. (After Borradaile and Potts, modified.)

**Family 2. TEREBELLIDÆ** (Fig. 221). — Long worms living in burrows or tubes; head with many long tentacular filaments, respiratory in function; usually several pairs of branching gills on segments just back of head; parapodia small. *Amphitrite ornata* is pinkish in color; up to 30 cm. long; and lives in a strong tube.

**Family 3. ARENICOLIDÆ.** — This family contains one genus. *Arenicola marina* (Figs. 222, 223) has a head without tentacles

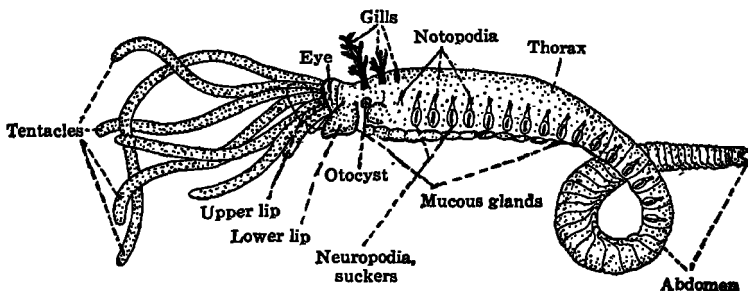
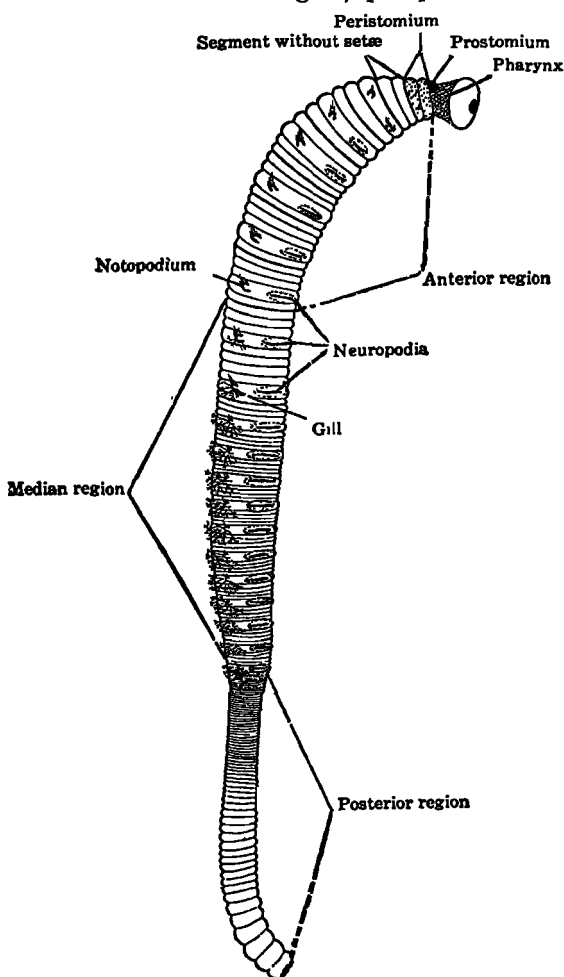


FIG. 221. — POLYCHÆTA. Family TEREBELLIDÆ. *Loimia*. Side view of a young worm removed from its tube. (After Wilson, modified.)

and a proboscis without jaws; the parapodia are rudimentary; branching gills are present above the parapodia of the middle

segments of the body. It reaches a length of 20 cm., and lives in deep burrows in the sand.

Family 4. SABELLIDÆ. — Worms with palps modified into semi-circular feathered gills; parapodia rudimentary; living in



membranous tubes. *Sabellia microphthalmia* is greenish-yellow in color and about 5 cm. long; the gill filaments are provided with minute eye spots; the tubes often encrust oyster shells.

Family 5. SERPULIDÆ. — These worms live in calcareous tubes; have prostomial palps modified into semi-circular feathered gills and dorsal gill filaments that serve as an operculum to close the opening to the tube. *Hydroides hexagonus* has usually purplish-brown gills; lives in a contorted tube encrusted on shells, etc.; and

FIG. 222. — POLYCHAETA. *Arenicola marina*. Side view.  
(After Ashworth, modified.)

is about 75 mm. long. *Spirorbis spirorbis* lives in a coiled tube, often forming a flat spiral, that is encrusted on seaweeds, etc.

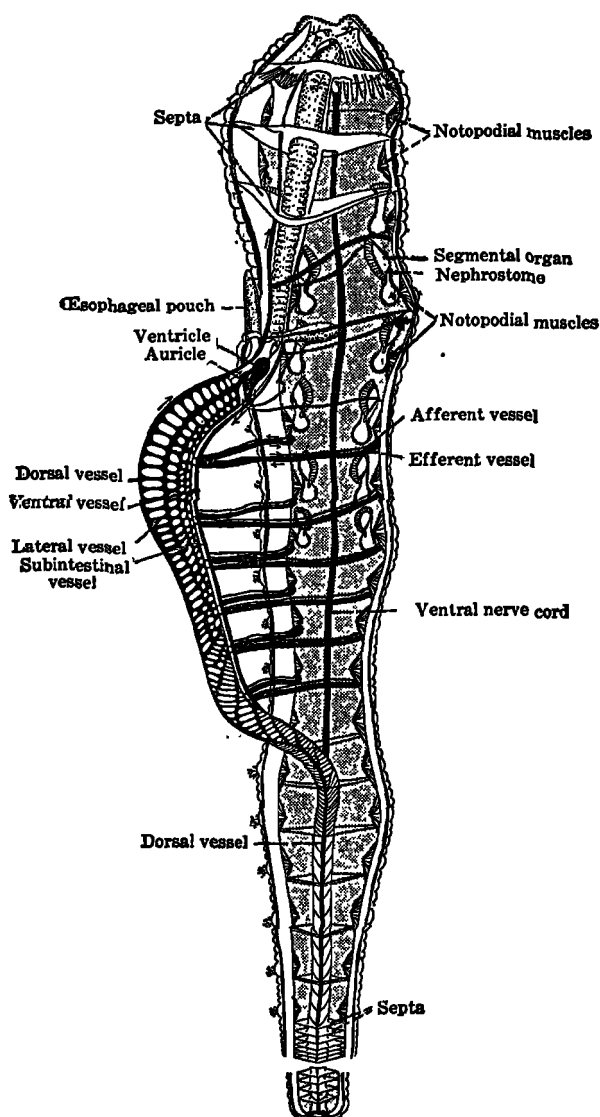


FIG. 223. — POLYCHAETA. *Arenicola marina*. Dissection to show internal organs. (After Ashworth, modified.)

**Order 2. OLIGOCHÆTA.** — Mostly terrestrial or aquatic in fresh water; no parapodia and few setæ; no distinct head with appendages; hermaphroditic; no trochophore larva. The oligochætes

may be divided into two suborders on the basis of habitat, size, number of segments, and character of reproduction.

**Suborder 1. MICRODRILI.** — Aquatic, small; few segments; often asexual reproduction. Among the families in this suborder are the following.

**Family 1. ÆOLOSO-MATIDÆ.** — Fresh-water worms; microscopic in size; four bundles of setæ in each segment; reproduction by asexual division. *Æolosoma quaternarium* (Fig. 224) is 1 mm. long and spotted with red oil globules in

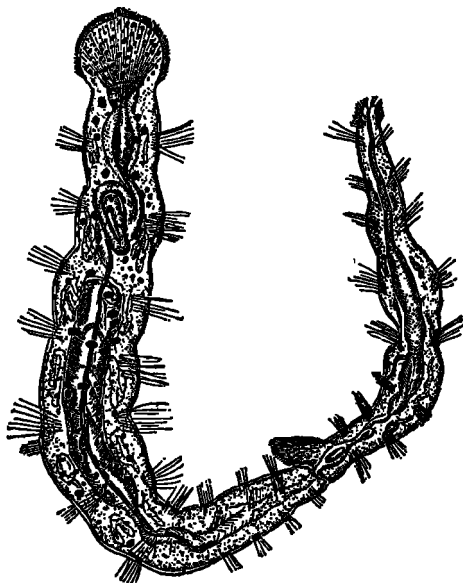


FIG. 224. — OLIGOCHÆTA: *Æolosoma* dividing transversely. (After Lankester.)

the integument; lives among algæ; and consists of from seven to ten segments.

**Family 2. DISCODRILIDÆ.** — Species parasitic on crayfishes; with sucker at the posterior end of the body; no setæ present; one dorsal and one ventral chitinous jaw. *Bdellodrilus philadelphicus* is 10 mm. long; the dorsal and ventral jaws are dissimilar; it lives principally on the ventral surface of the crayfish.

**Family 3. NAIDIDÆ.** — Aquatic, mostly in fresh water; small; transparent; two to four bundles of setæ on each segment, the ventral setæ forked; reproduction principally by transverse division, long chains of offspring formed. *Nais elinguis* (Fig. 225) is light brown in color; 2 to 4 mm. long; with 15 to 37 segments; head distinct; often among algæ. *Stylaria lacustris* is 25 mm. long; has a long, tentacle-like prostomium and 25 segments. *Dero limosa* is reddish in color; lives in tubes in ponds; has ciliated branchial appendages at posterior end; and consists of about 48

segments. *Chaetogaster limnæi* may be free-living or attached to or in the liver of fresh-water snails (*Lymnæa* or *Planorbis*); it is colorless; and has two bundles of ventral hooked setæ on each segment.

Family 4. TUBIFICIDÆ. — Fresh- and brackish-water species living in tubes; slender; with four bundles of setæ on each segment; no asexual reproduction by transverse division. *Tubifex tubifex* is reddish in color and about 4 cm. long; it occurs in patches on muddy bottoms where the posterior end of the body, which protrudes from the tube, is waved back and forth. *Limnodrilus claparedianus* lives in fresh water and is from 4 to 7 cm. long; the setæ are all forked; 150 segments present.

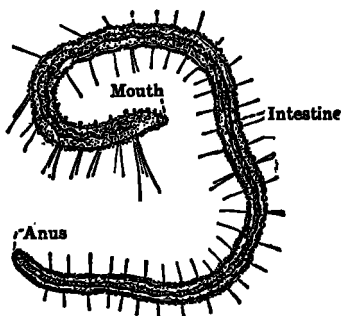


FIG. 225. — OLIGOCHÆTA. *Nais*.  
(After Leunis.)

Family 5. ENCHYTRÆIDÆ. — Both terrestrial and aquatic species; four bundles of hair-like setæ in each segment; usually whitish in appearance; up to 25 mm. long. *Enchytræus albidus* is milk-white, slender, and about 25 mm. long; it has from 53 to 69 segments, and the setæ are nearly straight and of equal length; it lives under débris along the seashore.

**Suborder 2. MEGADRILI.** — Usually terrestrial; large; many segments; reproduction, sexual.

Family 1. LUMBRICIDÆ. — Earthworms. *Lumbricus terrestris* (see p. 302). *Eisenia fetida* lives in manure and is pink in color with a dark ring on each segment. *Helodrilus caliginosus* lives in the soil and may be pink, blue, yellow, or gray in color.

Family 2. MEGASCOLECIDÆ. — Terrestrial, some species aquatic; many tropical species. *Diplocardia communis* is a North American species that lives in the soil, is flesh-colored, and about 30 cm. long.

## 2. CLASS II. ARCHIANNELIDA

This class contains half a dozen genera of annelids of which *Polygordius* is the best known. *Polygordius* (Fig. 226, A) is a marine worm living in the sand. It is about an inch and one half long, and only indistinctly segmented externally. The prostomium

bears a pair of tentacles. The mouth opening is in the ventral part of the first segment, and the anal opening in the last segment. A pair of ciliated pits, one on either side of the prostomium, probably serve as sense organs.

Internally *Polygordius* resembles the earthworm. The coelom is divided into compartments by septa. The internal organs are

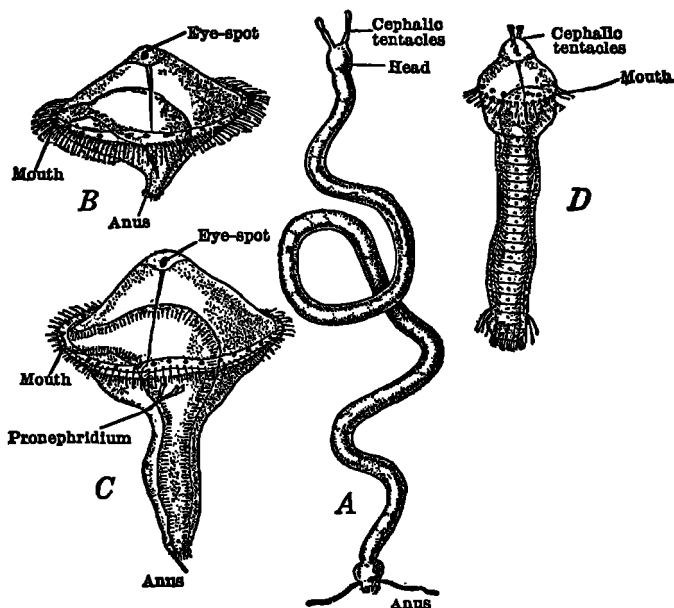


FIG. 226. — ARCHIAMNELIDA. *Polygordius appendiculatus*. A, dorsal view. B, trochophore larva. C and D, stages in development of trochophore into the worm. (After Fraipont, from Bourne.)

repeated so that almost every segment possesses coelomic cavities, longitudinal muscles, a pair of nephridia, a pair of gonads, a section of the alimentary canal, and part of the ventral nerve cord. The development of *Polygordius* includes a trochophore stage (Fig. 226, B). The adult develops from the trochophore by the growth and elongation of the anal end. This elongation becomes segmented and by continued growth transforms into the adult.

The archiamnelids are probably not primitive but are specialized in the direction of simplification and reduction. The genera may be arranged in a series beginning with *Polygordius* and ending with forms close to the CHÆTOPODA.



*Protodrilus* resembles *Polygordius* but has ciliated rings around the segments; a longitudinal ciliated groove in the mid-ventral line; and a ventral, muscular pharyngeal sac. *Protodrilus chætifer* has four short setæ in each segment. *Saccocirrus* has a single bundle of setæ on either side of each segment. *Nerilla* (Fig. 227) has two bundles of setæ separated by a cirrus on either side of each segment; a pair of palps and three prestomial tentacles.

The cell lineage of *Polygordius* has been worked out very thoroughly. (Woltereck.) Six synchronous cleavages divide the egg into 2, 4, 8, 16, 32, and 64 cells at which stage the embryo is a hollow spherical blastula. At about this time cilia grow out from the cells from which the prototroch of the trochophore larva will arise. After the 64-cell stage the macromeres give off a fifth quartet which will produce endoderm only. At about the 140-cell stage the blastula becomes much flattened and later invaginates into a gastrula. The blastopore takes on an oval shape and the cells on either side join thus forming two openings which in time form the mouth and anus. By rearrangement of the cells the gastrula changes into a trochophore which loses its flatness and becomes arched dorsally (Fig. 226, B). The fate of every cell has been followed from the cleavage of the egg to the trochophore stage and the development of the latter into the adult worm has also been carefully determined.

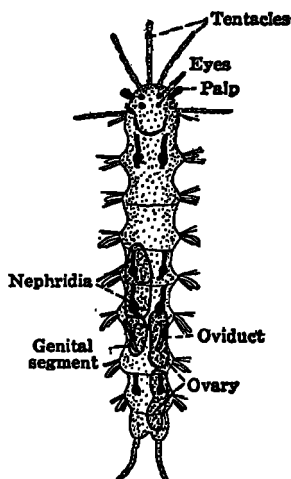


FIG. 227. — ARCHIANNELIDA. *Nerilla*. Dorsal view of female. (After Goodrich, modified.)

### 3. CLASS III. HIRUDINEA

#### (1) *HIRUDO MEDICINALIS* — THE MEDICINAL LEECH

The animals included in this class are commonly called *leeches*. They are usually flattened dorso-ventrally, but differ externally from the flatworms (PLATYHELMINTHES, Chap. V) in being distinctly segmented. The external segmentation, however, does not correspond exactly to the internal segmentation, since there are a variable number of external grooves (from two to fourteen) to

every real segment, *e.g.* usually five in the medicinal leech, *Hirudo* (Fig. 228), and its allies, and three in *Glossiphonia*. Anatomical features which distinguish the HIRUDINEA from the ARCHIANNELIDA and CHÆTPODA are (1) the presence of a definite number of segments (thirty-three), (2) two suckers, one found around the mouth and the other at the posterior end, and (3) the absence of setæ (except in one genus). They are hermaphrodites.

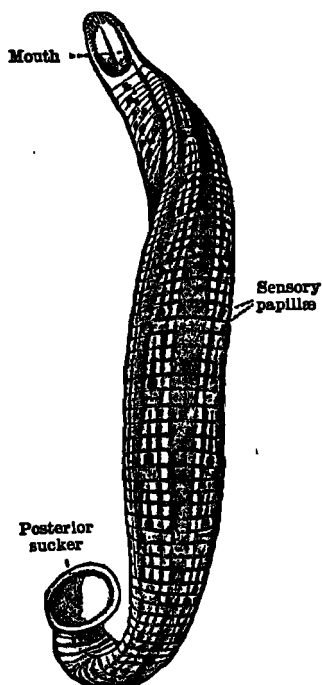


FIG. 228. — *Hirudo medicinalis*, the medicinal leech. (From Shipley and MacBride.)

*Hirudo medicinalis*, the medicinal leech (Fig. 228), is usually selected as an example of the class. It is about four inches long, but is capable of great contractions and elongation. The suckers are used as organs of attachment, and during locomotion are alternately fastened to and released from the substratum, the animal looping along like a measuring-worm. Leeches are also able to swim through the water by undulating movements.

The alimentary tract (Fig. 229) is fitted for the digestion of the blood of vertebrates, which forms the principal food of some leeches. The mouth lies in the anterior sucker and is provided with three jaws armed with chitinous teeth for biting. The blood flow caused by the bite of a leech is difficult to stop, since a secretion from glands opening near the jaws tends to prevent coagulation. Blood is sucked up by the dilation of the muscular pharynx. The short œsophagus leads from the pharynx into the crop, which has eleven pairs of lateral branches. Here the blood is stored until digested in the small globular stomach. A leech is able to ingest three times its own weight in blood, and, since it may take as long as nine months to digest this amount, meals are few and far between. The intestine leads directly to the anus.

The absorbed food passes into the blood vessels and the cœlomir

cavities, and is carried to all parts of the body. The coelom is usually small because of the development of a peculiar kind of connective tissue known as *botryoidal tissue*. The spaces in the body which are not filled up by this tissue are called sinuses, and in many species contain a fluid very much like true blood.

Respiration is carried on at the surface of the body, oxygen being taken into, and carbon dioxide given off by, many blood capillaries in the skin. Waste products are extracted from the blood and coelomic fluid by seventeen pairs of *nephridia* (Fig. 229) which resemble those of the earthworm (Fig. 209), but frequently lack the internal opening.

Leeches are *hermaphroditic*, but the eggs of one animal are fertilized by spermatozoa from another leech. The *spermatozoa* arise in the nine pairs of segmentally arranged *testes* (Fig. 229): they pass into the *vas deferens*, then into a convoluted tube called the *epididymus*, where they are fastened into bundles called *spermatophores*, and are finally deposited within the body of another leech by means of the muscular *penis*. The *eggs* arise in the *ovaries*

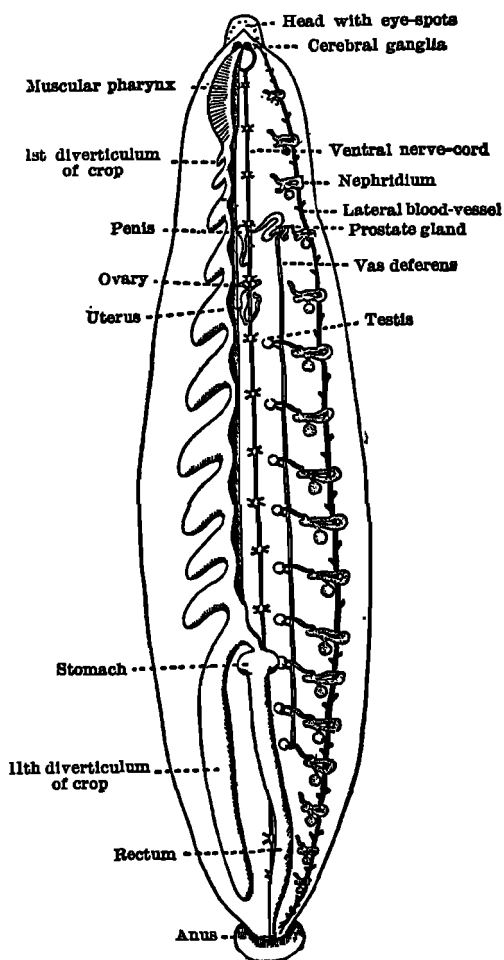


FIG. 229. — *Hirudo medicinalis*: internal organs.  
(From Shipley and MacBride.)

of which there is a single pair; they pass into the *oviducts*, then into the *uterus*, and finally out through the *genital pore* ventrally situated in segment XI. *Copulation* and the formation of a *cocoon* are similar to these processes in the earthworm (p. 310).

## (2) OTHER HIRUDINEA

*Hirudo medicinalis* (Figs. 228, 229) has served to illustrate the principal characteristics of this class. Variations from this type are indicated in the following descriptions. Two orders may be recognized. The fresh-water leeches of the genus *Acanthobdella*

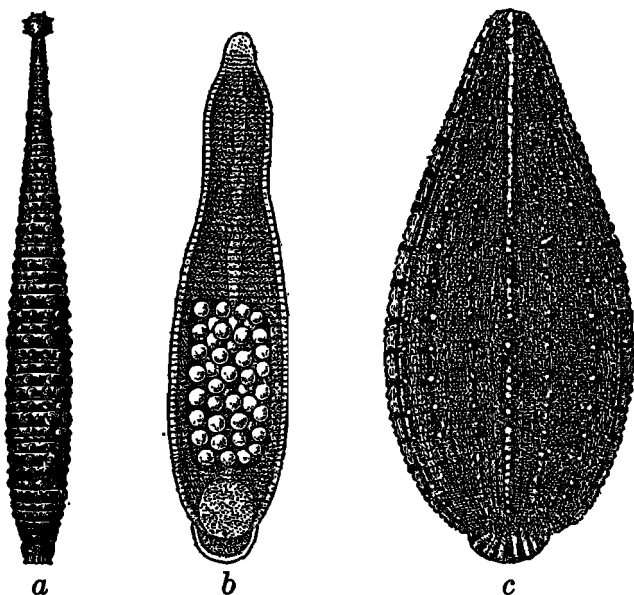


FIG. 230. — Leeches. a, *Pontobdella muricata*, a green-colored marine species that attacks rays and sharks. b, *Helobdella algira*, a species that transmits trypanosomes (see p. 47) to frogs. Ventral view showing eggs. c, *Placobdella catenigera*, a species that transmits haemogregarines (see p. 62) to tortoises. (a, after Bourne; b, c, after Brumpt.)

which are parasitic on salmon do not belong in either order but possess many chætopod characteristics and are sometimes included with the oligochætes.

**Order 1. RHYNCHOBDELLIDA.** — Leeches without jaws; proboscis can be protruded from mouth; blood, colorless; segments usually of 3 or 4, rarely 5, rings; fresh-water and salt-water species.

Family 1. **ICHTHYOBDELLIDÆ**. — Body long, narrowing toward anterior end; more than three rings in each body segment; suckers pedunculate. *Piscicola funduli* is parasitic on the fish, *Fundulus*; it has a cylindrical body colored light green and spotted with dots of green and brown and many rings in each segment. *Cystobranchus vividus* is also a parasite on *Fundulus*; it possesses eleven pairs of brownish or purplish papiliform gill-vesicles along the sides of the body.

Family 2. **GLOSSIPHONIDÆ**. — Fresh-water species; each segment with three rings; anterior sucker fused with the body; posterior sucker distinct. *Glossiphonia parasitica* (*Clepsine plana*) occurs under stones or attached to turtles. The body is broad and flat and greenish or yellowish in color. *Glossiphonia stagnalis* is a very active species that lives on snails. The body is grayish or pinkish in color. *Hemiclepsis carinata* attacks frogs and toads. It is greenish in color with longitudinal stripes and the anterior sucker is pedunculate.

Order 2. **GNATHOBDELLIDÆ**. — Leeches mostly with jaws; no proboscis present; blood, red; fresh-water and terrestrial species.

Family 1. **HIRUDINIDÆ**. — Each segment with five rings; three toothed jaws; five pairs of eyes. *Hirudo medicinalis* (p. 321). *Hæmopsis marmoratis*, the horse leech, is about 10 cm. long; it lives in mud near fresh water and feeds principally on worms, snails, etc., occasionally sucking blood. *Macrobdella decora* is very common in fresh water and sucks blood avidly from frogs, fish, cattle, man, etc., although it also eats other small animals.

Family 2. **HERPOBDELLIDÆ**. — Leeches with three muscular ridges in place of jaws. *Herpobdella punctata* is common in ponds and streams. It has three pairs of eyes; is about 8 cm. long; and is brownish-black in color with four rows of black spots along the dorsal surface.

#### 4. CLASS IV. GEPHYREA

The worm-like animals in this class may provisionally be included in the phylum ANNELIDA. They are comparatively large; have a large coelom; but have lost all or most of their segmentation. Two families may be recognized.

Family 1. **ECHIUROIDEA**. — These marine worms have traces of segmentation in the adult, a well-developed prestomium (a proboscis), a pair of ventral hooked setæ, and a terminal anus.

They usually live in crevices in rocks, using their proboscis for locomotion, for capturing prey, and as an organ of sense. There is a trochophore stage in development. *Echiurus pallasii* possesses a spoon-shaped proboscis and 22 body rings. In *Thalassema melitta*

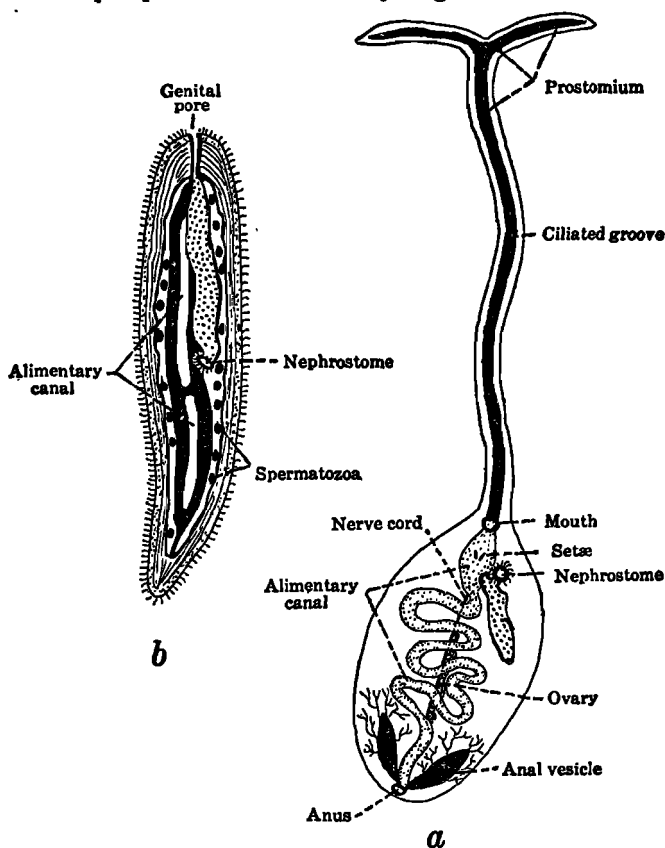


FIG. 231. — GEPHYREA. *Bonellia viridis*. a, Female. b, Male from nephridium of female. (After Spengler, modified.)

the proboscis is somewhat pointed. This species often occurs in sand-dollar shells. *Bonellia viridis* (Fig. 231) is supplied in the female with a very long proboscis which is bifurcated at the end; the male is a small turbellarian-like ciliated organism that lives in the segmental organ of the female.

Family 2. SIPUNCULOIDEA (Fig. 232). — These are unsegmented, with only one pair of nephridia, a large coelom, and an anus on the

dorsal surface near the anterior end. They live in the sand or bore into coral rock, and are capable of slow, creeping locomotion. The anterior part of the body can be drawn into the larger posterior portion, and is therefore called the introvert. Tentacles are usually present at the anterior end. *Phascolosoma gouldi* is about 18 cm. long, and has a smooth skin and many tentacles in several rows. *Phascolion strombi* uses a snail shell for protection, closing the entrance with a plug of sand, through a hole in which the introvert may be protruded. *Priapulus caudatus* occurs in the Arctic Seas. The pharynx is muscular and provided with numerous teeth and the anus is located at the posterior end. It lives in the mud or sand in shallow water with the anterior end projecting into the water.

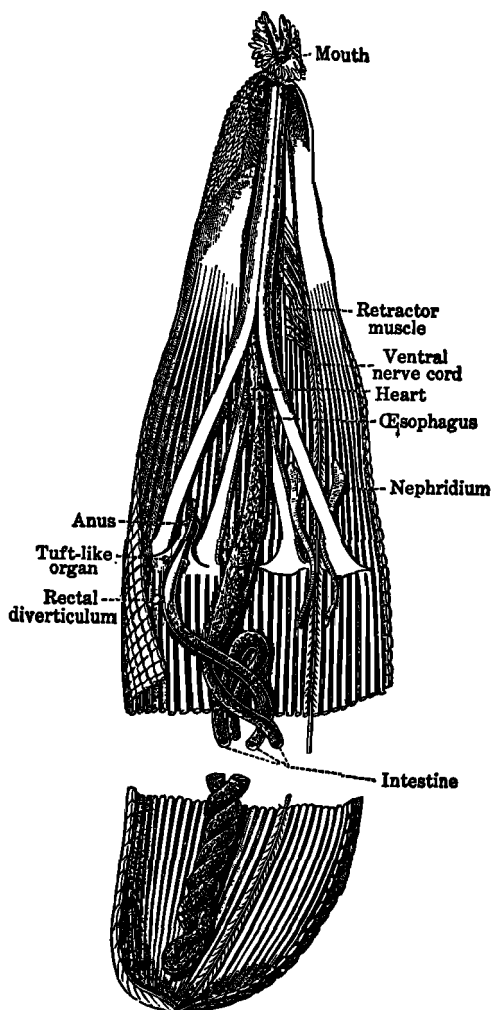


FIG. 232. — GEPHYREA. *Sipunculus nudus*, with introvert and head fully extended, laid open by an incision along the right side to show the internal organs. The spindle-muscle is seen overlying the rectum. (From Shipley.)

# 5. CLASS-V. MYZOSTOMARIA

These worms appear to represent a branch from the polychaetes modified for a parasitic existence on or within echinoderms,

especially crinoids. The body is externally unsegmented, flat, and oval or discoidal in shape (Fig. 233). Five pairs of parapodia armed with acicula and hooks are present on the ventral surface, and around the edge are usually 10 pairs of cirri. Alternating with the parapodia are normally 4 pairs of suckers.

The digestive system consists of a mouth on the ventral surface near the anterior end which opens into a retractile pharynx

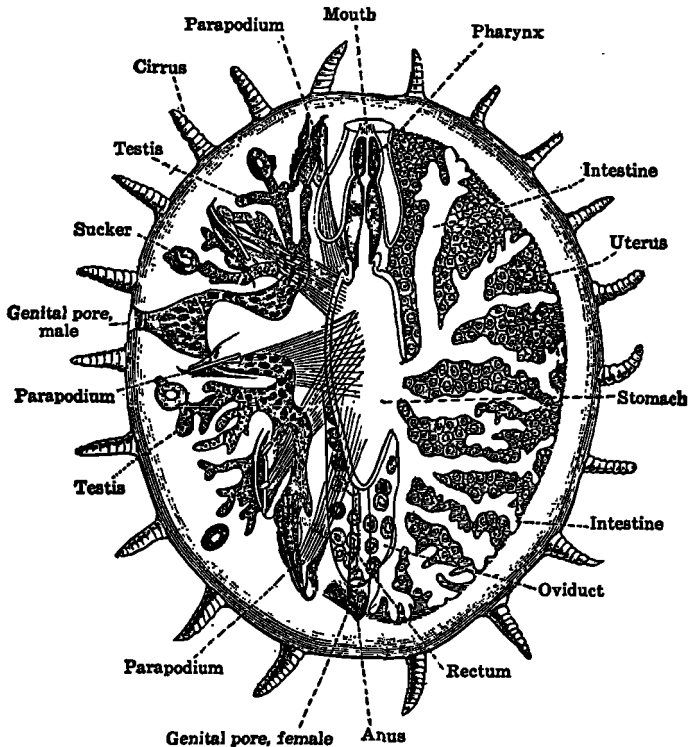


FIG. 233. — *Myzostoma cirriferum*. The organs are supposed to be seen by transparency. On the right side the more dorsal organs are shown, and on the left, those lying more ventrally. (After Lang and v. Graff.)

provided with a bulbous musculosus; next comes a short oesophagus, then the stomach, from which a number of ceca arise, and a straight intestine which ends in the anus on the ventral surface near the posterior end. The coelom is greatly reduced by parenchymous tissue. There is no circulatory system except a series of spaces filled with coelomic fluid. No special respiratory system is pres-



ent. In most species there is one pair of nephridia. The nervous system is well developed and of the ladder type. The worms are normally protandric hermaphrodites, functioning first as males and then as females. A trochophore larva of the annelid type develops from the egg.

Four families of MYZOSTOMARIA are recognized, the MYZOSTOMIDÆ, PROTOMYZOSTOMIDÆ, MESOMYZOSTOMIDÆ, and STELECHOPIDÆ. *Myzostoma cubanum* is a parasite of crinoids in the West Indies. It is about 1.7 mm. in diameter and has well-developed parapodia but no suckers. *Myzostoma glabrum* is a species that attaches itself to the oral plates of the crinoid, *Antedon rosacea*. It is nearly circular in outline and about 4 mm. long.

## 6. ANNELIDS IN GENERAL

**Morphology.**—Three morphological characteristics of the ANNELIDA are especially worthy of notice: (1) metamerism, (2) the coelom, and (3) the trochophore stage in development.

**Metamerism.**—The segmentation of the body as exhibited in annelids is called *metamerism*, and is here encountered for the first time. This type of structure is of considerable interest since the most successful groups in the animal kingdom, the ARTHROPODA and VERTEBRATA, have their parts metamerically arranged. How this condition has been brought about is still doubtful, but many theories have been proposed to account for it. According to one view the body of a metameric animal has evolved from that of a non-segmented animal by transverse fission. The individuals thus produced remained united end to end and gradually became integrated both morphologically and physiologically so that their individualities were united into one complex individuality. Some zoologists maintain that the segmental arrangement of organs such as nephridia, blood vessels, and reproductive organs has been caused by the division of a single ancestral organ, and not by the formation of new organs as the fission theory demands.

True metamerism, as exhibited by annelids, should not be confused with the *pseudometamerism* of the tapeworms (Fig. 164). The proglottids of the tapeworms are individuals budded off from the posterior end and differing from one another only in the degree of development. The tapeworm may be considered a row of incomplete individuals.

*The coelom.* — The coelom has already been defined as a cavity in the mesoderm lined by an epithelium; into it the excretory organs open, and from its walls the reproductive cells originate.

The importance of the coelom should be clearly understood, since it has played a prominent rôle in the progressive development of complexity of structure. The appearance of this cavity between the digestive tract and body wall brought about great physiological changes and is correlated with the origin of nephridia for transporting waste products out of the body, and of genital ducts for the exit of eggs and spermatozoa. The coelom also affected the distribution of nutritive substances within the body, since it contains a fluid which takes up material absorbed by the alimentary canal and carries it to the tissues. Excretory matter finds its way into the coelomic fluid and thence out of the body through the nephridia.

So important is the coelom considered by most zoologists that the METAZOA are frequently separated into two groups: (1) the ACCELOMATA without a coelom, and (2) the CŒLOMATA with a coelom. The PORIFERA, CŒLENTERATA, and CTENOPHORA are undoubtedly ACCELOMATA. Likewise the ANNELIDA, ECHINODERMATA, ARTHROPODA, MOLLUSCA, and CHORDATA are certainly CŒLOMATA. But whether the PLATYHELMINTHES, NEMATHELMINTHES, and a number of other groups possess a coelom is still uncertain.

*The trochophore.* — The term *trochophore* has been applied to the larval stages of a number of marine animals. The description and figures of the development of *Polygordius* (p. 320, Fig. 226) are sufficient to indicate the peculiarities of this larva.

Many other marine annelids pass through a trochophore stage during their life history; those that do not are supposed to have lost this step during the course of evolution.

Since a trochophore also appears in the development of animals belonging to other groups, for example, MOLLUSCA, NEMERTINEA, and BRYOZOA, and resembles very closely certain ROTIFERA, the conclusion has been reached by some embryologists that these groups of animals are all descended from a common hypothetical ancestor, the trochozoon. Strong arguments have been advanced both for and against this theory.

**Interrelations and phylogeny of the annelids.**—The polychætes appear to be the simplest of the annelids. They are marine animals as were probably their ancestors. The oligochætes evolved

from the polychætes as the latter adopted fresh-water and terrestrial habitats. The archiannelids, as already pointed out, seem likewise to have arisen from the polychætes; in fact, some of the groups of worms ordinarily included in the class POLYCHÆTA, such as the ÆOLOSOVIDÆ, are considered by others to be archiannelids. The HIRUDINEA have many characteristics in common with the oligochætes and are believed to be derived from them. The genus *Acanthobdella* is included by some in the HIRUDINEA and by others in the OLIGOCHÆTA; and the DISCODRILIDÆ, which are now placed with the oligochætes, possess a sucker at the posterior end of the body and were formerly included with the leeches. The GEPHYREA possess sufficient annelid characteristics to justify their inclusion in this phylum. They seem to have evolved from the CHÆTOPODA but have lost many of the features of this class, probably as a result of their sedentary mode of life.

The history of our knowledge of the annelida. — The annelids were by early zoologists included with other worms in the group VERMES but were separated by Cuvier in 1798 from the unsegmented worms and designated by Lamarck the ANNELIDS. This group was sometime later (1820) divided by Savigny into 4 subdivisions, (1) the NEREIDÆ, (2) the SERPULEÆ, (3) the LUMBRICINÆ, and (4) the HIRUDINÆ. The terms POLYCHÆTA and OLIGOCHÆTA we owe to Grube (1851).

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# CHAPTER IX

## PHYLUM MOLLUSCA

### INTRODUCTION

The phylum MOLLUSCA includes the snails, slugs, clams, oysters, octopods, and nautili. They are primitively bilaterally symmetrical, but unsegmented, and many of them possess a shell of calcium carbonate. Mussels, clams, snails, and squids do not appear at first sight to have much in common, but a closer examination reveals several structures possessed by all. One of these is an organ called the *foot*, which in the snail (Fig. 234, *I*) is usually used for creeping over surfaces, in the clam (*II*) generally for plowing through the mud, and in the squid (*III*) for seizing prey. In each there is a space called the *mantle cavity* between the main body and an enclosing envelope, the *mantle*. The *anus* opens into the mantle cavity.

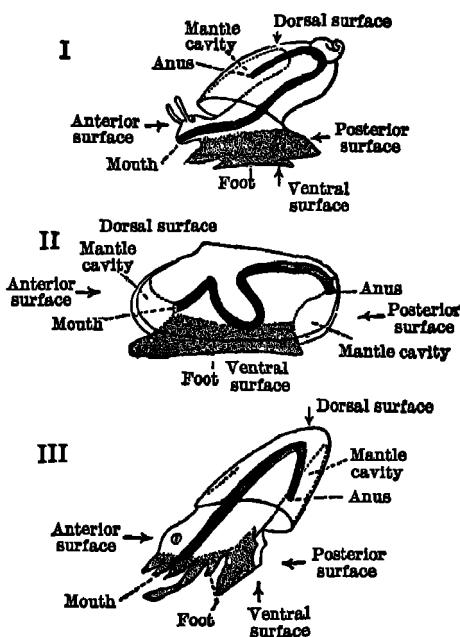


FIG. 234. — Diagrams of three types of mollusks. — I, a PROSOBRANCH GASTROPOD; II, a LAMELLIBRANCH, and III; a CEPHALOPOD, to show the form of the foot and its relations and the relations of the visceral hump to the anteroposterior and dorsoventral axes. (From Shipley and MacBride, after Lankester.)

The mollusks are divided into five classes according to their symmetry and the characters of the foot, shell, mantle, gills, and nervous system.

**Definition.** — Phylum MOLLUSCA. — CLAMS, SNAILS, SQUIDS, OCTOPI. — Triploblastic, bilaterally symmetrical animals; anus and coelom present; no segmentation; shell usually present; the characteristic organ is a ventral muscular foot.

CLASS I. AMPHINEURA, the chitons, with bilateral symmetry, often a shell of eight transverse calcareous plates, and many pairs of gill filaments;

CLASS II. GASTROPODA, the snails, slugs, whelks, etc., with asymmetry and usually a spirally coiled shell;

CLASS III. SCAPHOPODA, the elephants'-tusk shells, with tubular shell and mantle;

CLASS IV. CEPHALOPODA, the squids, cuttlefishes, octopods, and nautili, with bilateral symmetry, a foot divided into arms provided with suckers, and a well-developed nervous system concentrated in the head;

CLASS V. PELECYPODA, the clams, mussels, oysters, and scallops, usually with bilateral symmetry, a shell of two valves, and a mantle of two lobes.

### 1. CLASS I. AMPHINEURA

This class contains about 700 species of marine mollusks that live usually on the bottom near the shore. The *body* (Fig. 235) is

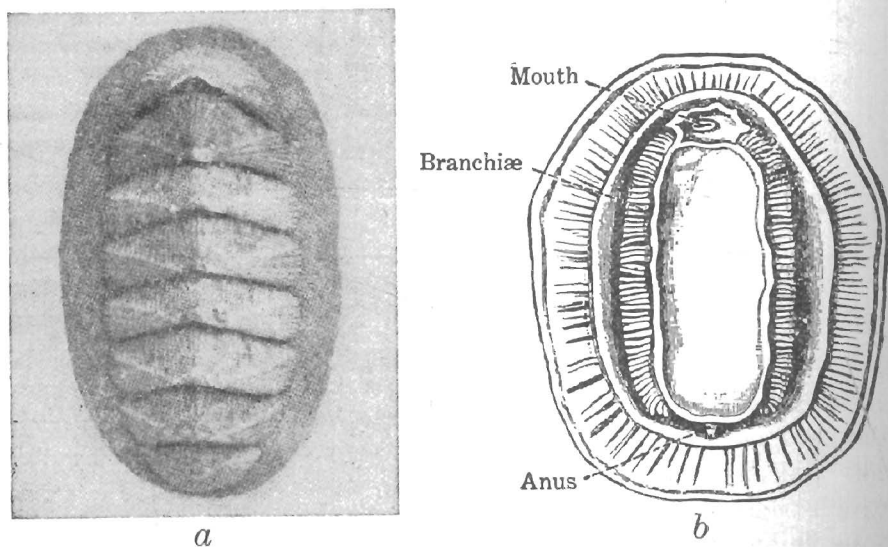


FIG. 235. — AMPHINEURA. a, *Ischnochiton cooperi*: dorsal view. b, *Chiton squamosus*: ventral view. (a, from Johnson and Snook; b, from Cooke.)

elongated and bilaterally symmetrical with the *mouth* at one end and the *anus* at the other end. The *head*, which is sheltered by the mouth, is usually not well developed and lacks both tentacles and eyes. The dorsal surface is occupied by the *mantle*, in which calcareous spicules are embedded and sometimes a continuous

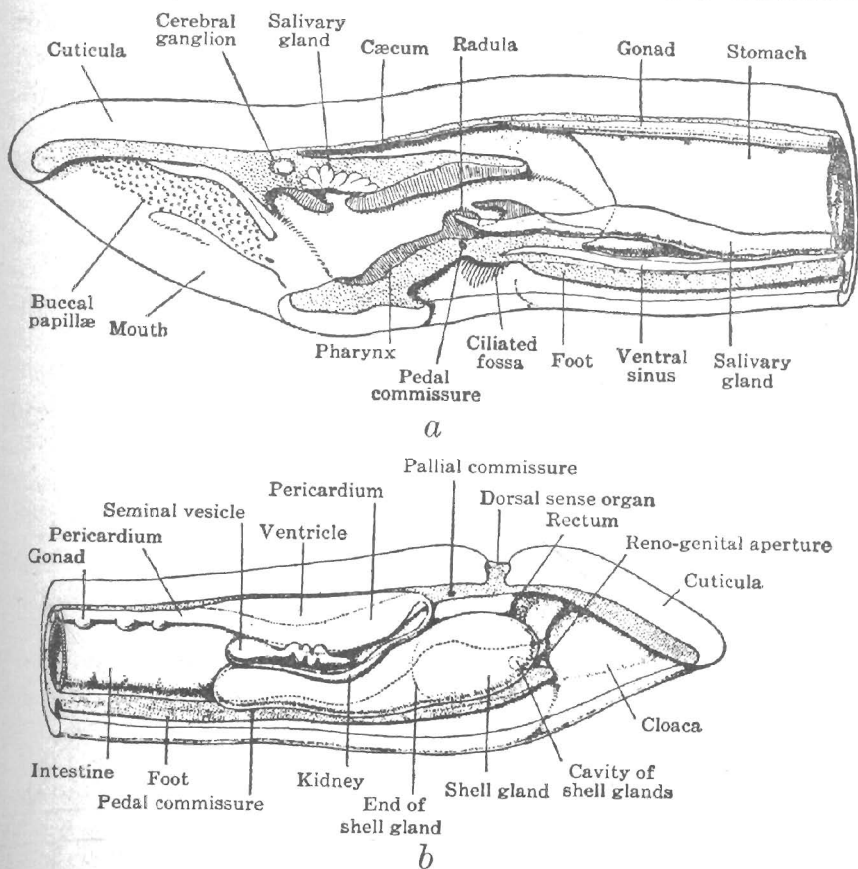


FIG. 236. — AMPHINEURA. *Proneomenia gerlachei*. a, Right half of anterior part of body; left-side view. b, Right half of posterior part of body: left-side view. (From Cooke.)

covering of plates (Fig. 235, a). A narrow *mantle cavity* extends along the sides of the body; that part of the mantle that forms this cavity is known as the *girdle*. The *foot* is flat. A *radula* (Fig. 236) is usually present. The *nervous system* consists of a circum-oesophageal ring and two pairs of longitudinal cords which innervate the foot (pedal) and mantle (pallial). No definite ganglia are present but the nerve cords are supplied with ganglion cells. In

the chitons the valves of the shell are pierced by branching canals through which nerves reach the surface of the mantle where they connect with sense organs called shell-eyes.

The *alimentary canal* (Fig. 236) extends in a straight line from the mouth to the anus; into it, open ducts from mucous, salivary, and hepatic glands. There is a heart near the posterior end, an aorta, and two large sinuses. The blood is, of course, oxygenated in the gills. Two kidneys are present; each possesses a duct that opens outside the body near the posterior end and a duct that opens into the pericardium. The eggs usually give rise to trochophore larvæ. Chitons occur as fossils in the Ordovician period.

The AMPHINEURA may be divided into two orders.

**Order 1. POLYPLACOPHORA.** — These are known as chitons. They are elliptical in outline, have a flat foot which occupies the entire ventral surface, and a convex dorsal surface characterized by a series of eight transverse overlapping calcareous plates. The mantle groove contains from four to eighty pairs of ctenidium-like gills. Chitons creep about slowly on the sea bottom giving preference to smooth stones. The overlapping valves of the shell allow them to bend the body and even to roll up into a ball. They feed chiefly on algæ. The sexes are separate.

*Chætopleura apiculata* is a chiton that is common in shallow water along the Atlantic coast from Cape Cod to Florida. It is oval in shape and about 17 mm. long and 10 mm. broad. *Chiton tuberculatus* is common in the West Indies. It is about 8 cm. long and 0.5 cm. broad.

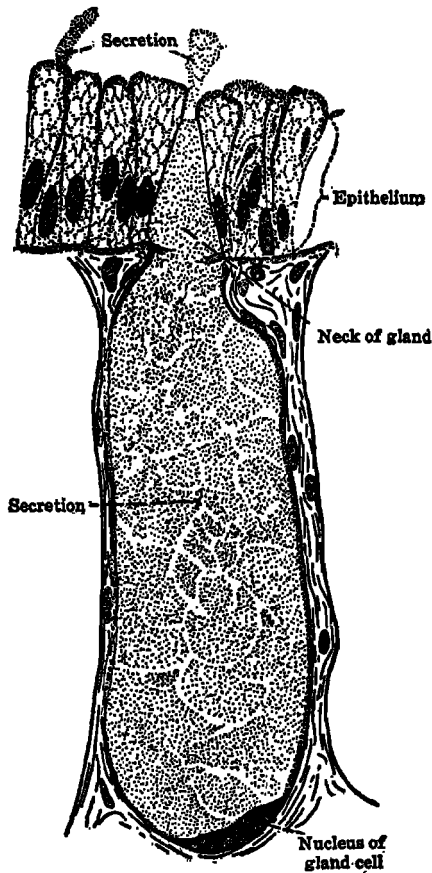
**Order 2. APLACOPHORA.** — The name SOLENOGASTRES is also used for this order. They are often worm-like in appearance; the shell is absent; the foot is reduced or lost; the radula may be reduced or absent; the gills are located in the cloaca. Certain species live among corals and hydroids and eat these polyps, and other species feed on protozoons and other minute organisms. This order is believed by some zoologists to be more closely allied with the primitive worms, such as the ARCHIANNELIDA, than with the mollusks. *Neomenia carinata* is a species living in the North Atlantic; it has a short, thick body about 2.5 cm. long; is covered with spicules; but lacks a radula. *Chætoderma nitidulum* occurs in the Gulf of Maine and elsewhere; it is slender and worm-like, being about 25 mm. long and only 2 mm. broad.



2. CLASS II. GASTROPODA

(1) *HELIX POMATIA* — A TERRESTRIAL SNAIL

**External features.** — The body of a snail consists of a *head*, *neck*, *foot*, and *visceral hump*, as shown in Plate II. The *head* bears two pairs of *tentacles*: (1) a short anterior pair containing the olfactory nerves, and (2) a longer pair containing the *eyes*. The *mouth* is in front and below the tentacles, and just beneath the mouth is the opening of the pedal *mucous gland*. The *foot* is broad and flat; it is a muscular organ of locomotion with a mucous-secreting integument (Fig. 237). Both the foot and head may be withdrawn into the *shell*.



The *spiral shell* encloses the visceral hump, consisting of parts of the digestive, circulatory, respiratory, excretory, and reproductive systems. The *mantle* lines the shell, and is thin except where it joins the foot; here it forms a thick collar which secretes most of the shell. An opening beneath this collar is the *respiratory aperture* leading into the mantle cavity. The *anus* opens just back of this aperture. The *genital pore* is on the side of the head.

FIG. 237. — Mucous cell from the edge of the mantle of a terrestrial snail. (From Dahlgren and Kepner.)

**Anatomy and physiology.** — *Digestion.* — The general anatomy of a snail is shown in Plate II. The *digestive organs* include a

*buccal mass, œsophagus, salivary glands, crop, stomach, digestive glands, intestine, rectum, and anus.*

The food is chiefly, if not entirely, vegetation, such as lettuce. This is scraped up by a horny jaw or *mandible* and devoured after being rasped into fine particles by a band of teeth termed the *radula* (Fig. 238). The radula and the cartilages and muscles that move it backward and forward constitute the buccal mass. The

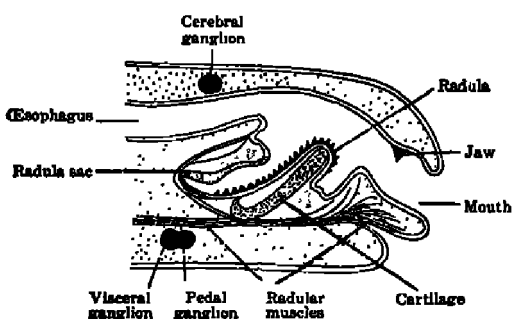


FIG. 238. — *Helix*, a snail. Vertical longitudinal section through head. (After Meisenheimer, modified.)

*salivary glands* which lie one on either side of the crop pour their secretion by means of the *salivary ducts* into the buccal cavity, where it is mixed with the food.

The *œsophagus* leads to the *crop*, and from here the food enters the *stomach*. The two *digestive glands* occupy a large part of the visceral hump. They secrete a diastatic ferment which converts starchy matters into glucose, and are comparable to the pancreas in vertebrate animals. This secretion enters the stomach and aids in digestion. Absorption takes place chiefly in the *intestine*, and the feces pass out through the *anus*.

*Circulation and respiration.* — The blood of the snail consists of a colorless plasma containing corpuscles, and serves to transport nutriment, oxygen, and waste products from one part of the body to another. The heart lies in the *pericardial cavity* (Plate II). The muscular *ventricle* forces the blood through the blood vessels by rhythmical pulsations. One large *aorta* arises at the apex of the ventricle; this gives rise at once to a *posterior branch*, which supplies chiefly the digestive gland, stomach, and ovotestis, and an *anterior branch* which carries blood to the head and foot. The blood passes from the arterial capillaries into *venous capillaries* and flows through these into *sinuses*. *Veins* lead from these sinuses to the walls of the mantle cavity, where the blood, after taking in oxygen and giving off carbon dioxide, enters the *pulmonary vein* and is carried to the single *auricle* and finally into the ventricle again.

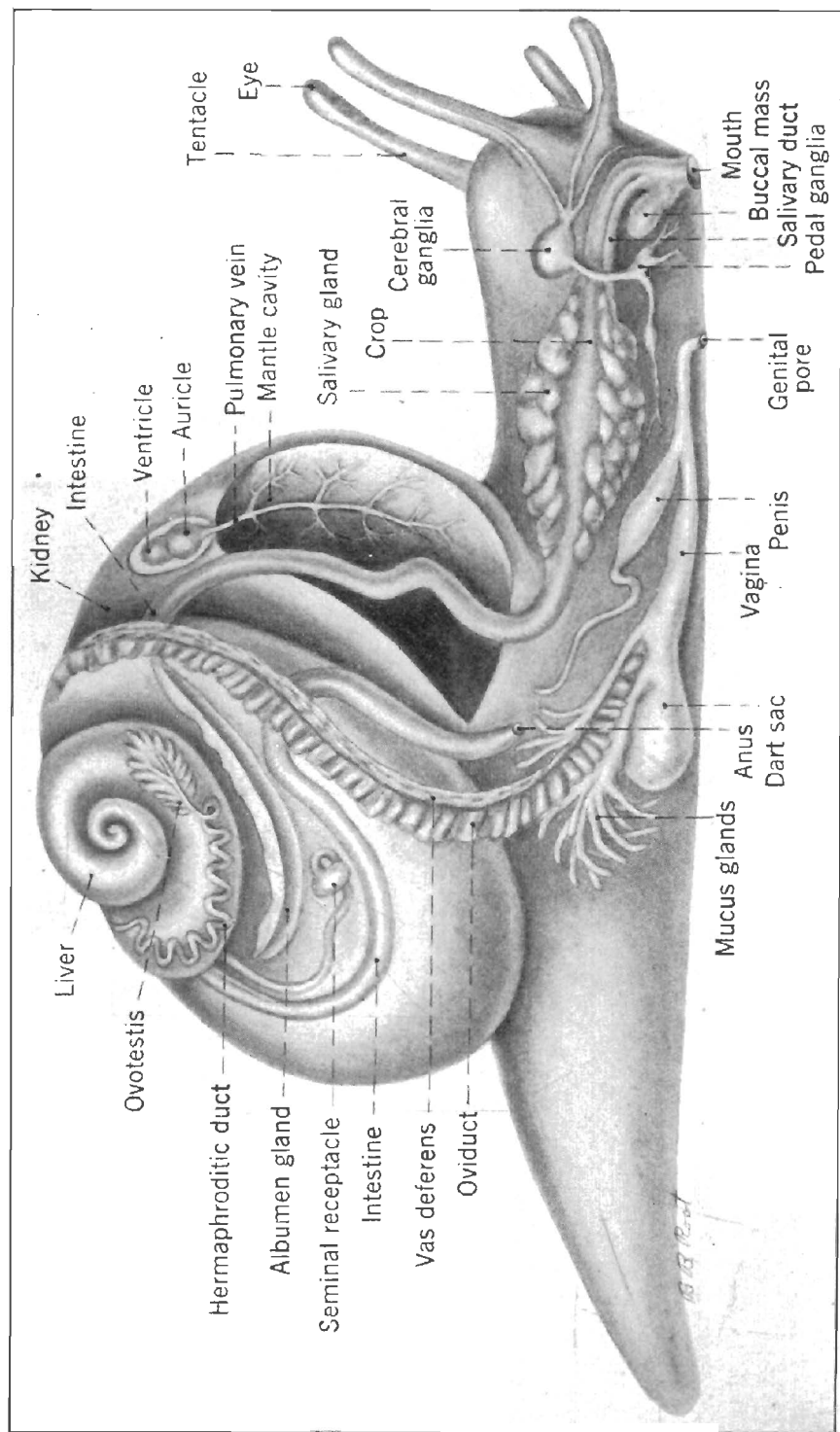


PLATE II. Side view of a Snail with shell removed showing internal organs. (Drawn by Barbara Bradley Root.)

**Excretion.** — The glandular *kidney* lies near the heart. Its duct, the *ureter* or *renal duct*, runs along beside the rectum and opens near the anus.

**Nervous system** (Plate II; Figs. 239, 240). — Most of the nervous tissue of the snail is concentrated just back of the buccal mass and

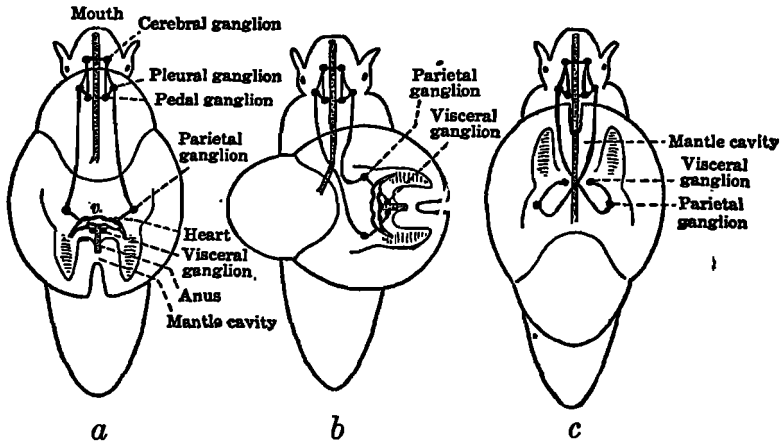


FIG. 239. — Nervous system of GASTROPODA as related to torsion. a, Supposed ancestral condition. b, Torsion 90°. c, Torsion 180°. (After Naef, from Borradaile and Potts, modified.)

forms a ring about the oesophagus. There are five sets of ganglia and four ganglionic swellings. The *supraoesophageal* or *cerebral ganglia* are paired and lie above the oesophagus. Nerves extend anteriorly from them, ending in the two *buccal ganglia*, the two *eyes*,

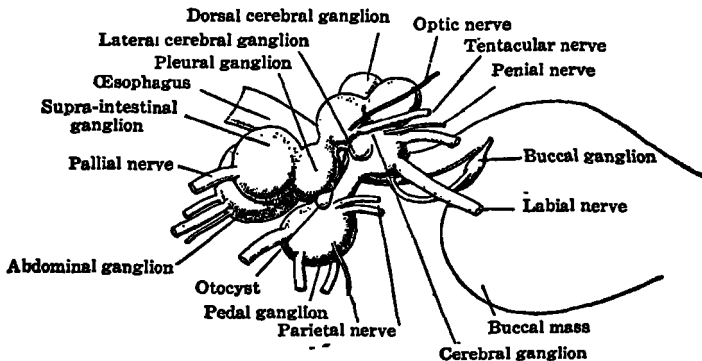


FIG. 240. — *Lymnaea stagnalis*: central nervous system, right-side view. (From Pelseneer.)

the two *ocular ganglionic swellings*, the two *olfactory ganglionic swellings*, and the mouth. Nerves called commissures connect the supracæsophageal ganglia with the ganglia which lie beneath the oesophagus. Here are four pairs of ganglia lying close together — the *pedal*, *pleural*, *parietal*, and *visceral*. Nerves pass from them to the visceral hump and the basal parts of the body.

*Sense organs.* — Both the foot and the tentacles are sensitive to contact, and are liberally supplied with nerves. Each long tentacle bears an *eye*. These eyes are probably not organs of sight, but only

sensitive to light of certain intensities. Many snails feed mostly at night, and their eyes may be adapted to dim light.

Snails possess a sense of *smell*, since some of them are able to locate food, which is hidden from sight, at a distance of eighteen inches. We are not certain where the sense of smell is located, but investigators are in-

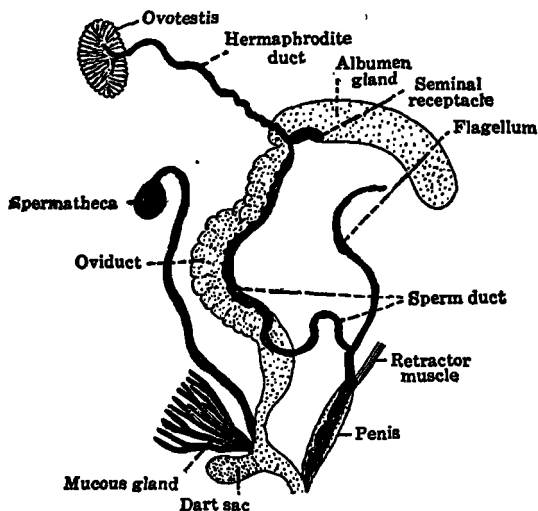


FIG. 241. — *Helix*, a snail. Reproductive organs.  
(After Meisenheimer, modified.)

clined to believe that the small tentacles are the *olfactory organs*. A sense of *taste* is doubtful.

There are two organs of equilibrium (*statocysts*), one on either side of the supracæsophageal ganglia. They are minute vesicles containing a fluid in which are suspended small calcareous bodies (*statoliths*). Nerves connect them with the supracæsophageal ganglia.

*Locomotion.* — The snail moves from place to place with a gliding motion. The slime gland which opens just beneath the mouth deposits a film of slime, and on this the animal moves by means of wave-like contractions of the longitudinal muscular fibers of the

foot. *Snails* have been observed to travel two inches per minute. (Baker.)

*Reproduction.* — Some gastropods are dicecious; others are monœcious. *Helix* is *hermaphroditic*, but the union of two animals is necessary for the fertilization of the eggs, since the spermatozoa of an individual do not unite with the eggs of the same animal. The *spermatozoa* arise in the *ovotestis* (Fig. 241); they pass through the coiled *hermaphroditic duct* and into the *sperm duct*; they then enter the *vas deferens* and are transferred to the *vagina* of another animal by means of a cylindrical *penis* which is protruded from the *genital pore*.

The *eggs* also arise in the *ovotestis* and are carried through the *hermaphroditic duct*; they receive material from the *albumen gland* and then pass into the *uterine canal*; they move from here down the *oviduct* into the *vagina*, where they are *fertilized* by spermatozoa which was transferred to the *seminal receptacle* by another snail. In almost all other land pulmonates impregnation is mutual, each animal acting during copulation as both male and female.

## (2) OTHER GASTROPODA

The gastropods are mollusks that have become modified from the bilaterally symmetrical, unsegmented condition of their ancestors as a result of the coiling of the visceral hump and the rotation of this structure in a counter-clockwise direction through an angle of 180°. The foot is flat for creeping; the head is distinct and bears eyes and tentacles; usually a shell of one piece; radula present; nervous system with cerebral, pleural, visceral, and usually pedal ganglia and a visceral loop; visceral hump often coiled; in some species a trochophore larva.

Gastropods are essentially aquatic animals, although some of them live in moist places on land or have means of preventing the escape of moisture from the body such as the epiphragm of certain snails. A few are parasitic on the outside or inside of other animals. Both unisexual and hermaphroditic gastropods occur; most species are oviparous but a few are viviparous. Variations from the type are indicated in the following paragraphs. No classification of this group is accepted by zoologists in general; the arrangement used here includes three orders, a number of suborders, and some of the more important families.\*

\* The author is indebted to Dr. Paul Bartsch for suggestions regarding the classification adopted

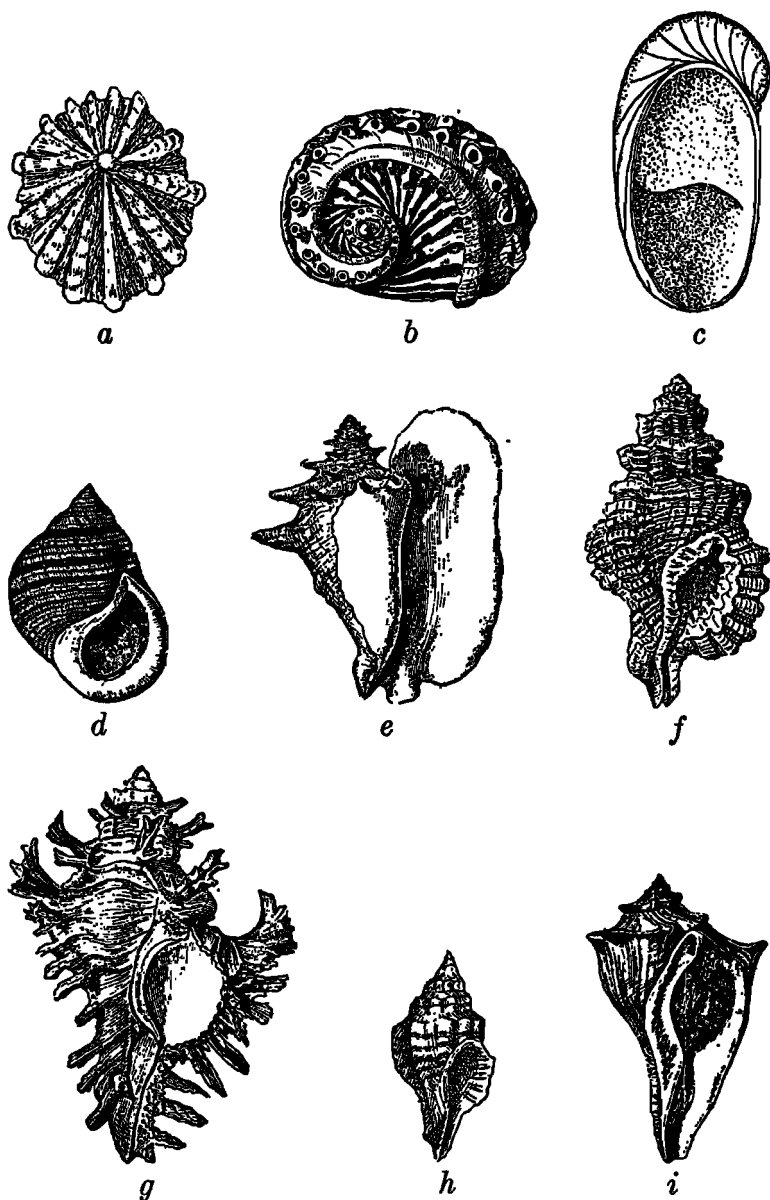


FIG. 242. — PROSOBRANCHIA: a-b, ASPIDOBANCHIA; c-i, PECTINIBRANCHIA: Types of shells. a, *Acmaea*. b, *Haliotis*. c, *Crepidula*. d, *Littorina*. e, *Strombus*. f, *Charonia*. g, *Murex*. h, *Urosalpinx*. i, *Busycon*. (From Tryon.)

**Order 1. PROSOBRANCHIA (STREPTONEURA).** — This large order contains the majority of the gastropods, about 30,000 species, most of which are marine. The gills are in the mantle cavity anterior to the heart (hence PROSOBRANCHIA) and the visceral hump is coiled (hence STREPTONEURA). The visceral connectives are usually twisted into a figure 8. The sexes are separate.

**Suborder 1. ASPIDOBANCHIA (SCUTIBRANCHIA).** — Primitive snails with usually two gills, two auricles, and two nephridia. The gonad opens to the outside through the right nephridium.

**Family 1. Acmæidæ (Fig. 242, a).** — Limpets. Marine; shell conical, no spiral; one gill; one auricle. Ex. *Acmæa testudinalis*; common on rocks in shallow water from Cape Cod northward.

**Family 2. Haliotidæ (Fig. 242, b).** — Ear Shells. Marine; shell with flat spiral, very large aperture; spiral series of holes near left margin; two gills, right gill small; two auricles; two nephridia; foot very large, with epipodia projecting through holes in shell. Ex. *Haliotis rufescens*: red abalone, common along coast of California south of Cape Mendocino; the flesh of this and other abalones is dried and sent to Japan; the shells are made into buttons, buckles, or used for inlaying.

**Family 3. Trochidæ.** — Marine; shell usually conical; horny operculum present; one gill. Ex. *Trochus niloticus*: shell pyramidal, of value as ornament; Indian Ocean. *Margarites obscurus*: shell conical; Long Island Sound northward.

**Family 4. Helicindæ.** — Terrestrial, in warm regions; shell conical; operculum oval or triangular; no gills, mantle cavity serving as lung. Ex. *Helicina orbiculata*: in the United States south of Tennessee.

**Suborder 2. PECTINIBRANCHIA.** — Snails with one auricle, one nephridium, and one gill; gill feathered on one side; gonad opens through separate duct. Most of the PROSOBRANCHIA belong to this suborder.

**Family 1. Capulidæ (Fig. 242, c).** — Shell with inconspicuous or no spiral, but with internal shelf; operculum absent; foot broad; sedentary, attached to rocks. Ex. *Crepidula fornicata*: shell convex, with slight spiral; shelf concave, white; Nova Scotia southward, in shallow water.

**Family 2. Littorinidæ.** — Periwinkles. Salt, brackish, and fresh water; shell conical and spiral; operculum horny; eyes at base of tentacles. Ex. *Littorina litorea* (Fig. 242, d): European edible



periwinkle; introduced and common from Delaware Bay northward.

Family 3. VIVIPARIDÆ. — Fresh water; cosmopolitan; shell conical; operculum horny; eyes on short stalks; viviparous. Ex. *Campeloma ponderosum* (Fig. 243): shell thick and solid; no umbilicus (cavity in columella); aperture ovate, longer than spire; New York to Illinois southward.

Family 4. PLEUROCERIDÆ. — Fresh water; all in North America, mostly in southern states; shell conical, elongate; operculum

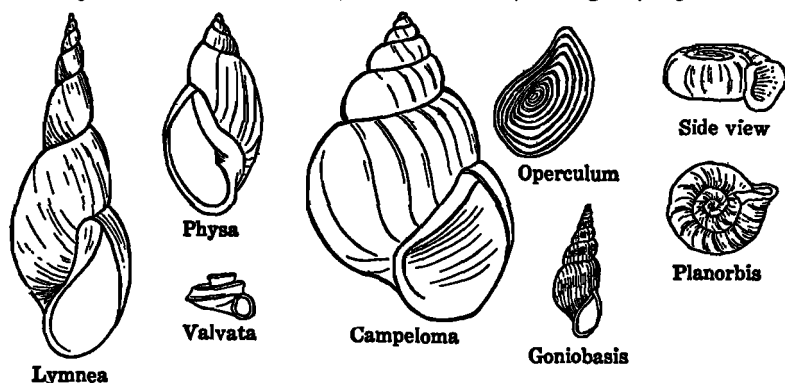


FIG. 243. — Some common genera of fresh-water gastropods.  
(From the General Biological Supply House.)

present; eyes sessile, at base of tentacles. Ex. *Pleurocera subulare*: long, tapering spire; Great Lakes region. *Goniobasis livescens* (Fig. 243): long, rather heavy shell; Great Lakes region.

Family 5. STROMBIDÆ (Fig. 242, e). — Marine; shell usually large, solid, with large lower whorl and expanded lip; foot long, narrow, for springing; eyes at end of stalks; in warm seas. Ex. *Strombus gigas*: conch; largest mollusk in the United States; about 25 cm. long; shell heavy, up to five pounds; flesh edible; shell used as horn and for making ornaments.

Family 6. CYMATHIDÆ (Fig. 242, f). — Tritons. Tropical seas. Ex. *Charonia (Triton) nodifera*: length 45 cm.; shell used as war horn or shepherd's horn.

Family 7. EULIMIDÆ. — Shell elongate; foot long and narrow; proboscis very long; often parasitic. Ex. *Stylifer stimpsoni*: parasitic on *Strongylocentrotus*.

Family 8. MURICIDÆ (Fig. 242, g). — Shell rough, with rows of protuberances; central tooth of radula with three cusps; mostly

tropical; food mostly other mollusks. Ex. *Urosalpinx cinereus* (Fig. 242, *h*): oyster drill; drills hole through oyster shell with radula in the proboscis; Massachusetts to Florida.

Family 9. BUCCINIDÆ (Fig. 242, *i*). — Whelks. Marine. Ex. *Buccinum undatum*: New Jersey northward; used as bait for cod, and

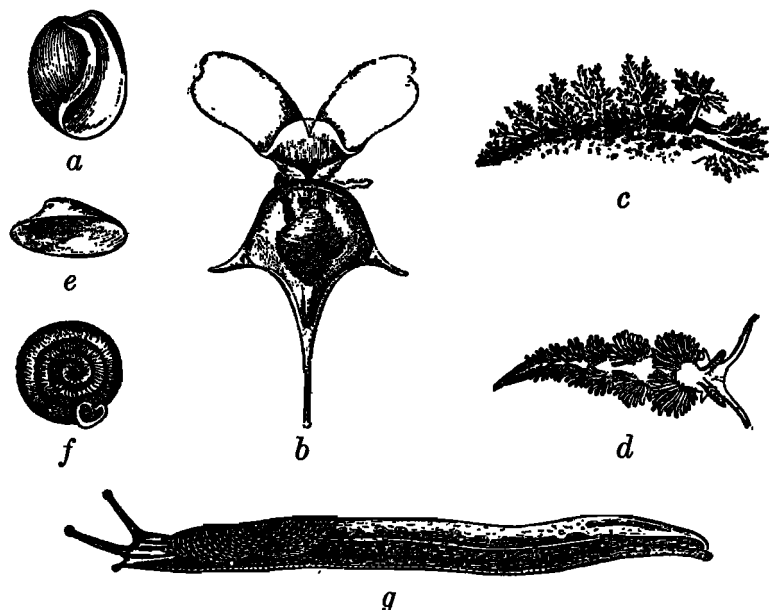


FIG. 244. — OPISTHOBRANCHIA: a-b, TECTIBRANCHIA; c-d, NUDIBRANCHIA; e-g, PULMONATA. a, *Haminea*. b, *Cavolinia*. c, *Dendronotus*. d, *Aeolis*. e, *Ancylus*. f, *Polygyra*. g, *Limax*. (From Tyron.)

in Europe as food for man. *Busycon canaliculatum*: conch; marine; large, heavy shell; long siphonal canal; Cape Cod southward.

Order 2. OPISTHOBRANCHIA. — Sea Slugs. This order is sometimes included with the order PULMONATA in a subclass EUTHYNEURA. They are all marine; shell small or absent; gill when present, posterior to the heart; visceral connectives not twisted; hermaphroditic; mostly live among seaweed and under stones near shore, some pelagic; food chiefly animal; two suborders.

Suborder 1. TECTIBRANCHIA. — Shell usually present; gills in mantle cavity.

Family 1. AKERIDÆ (Fig. 244, *a*). — Shell external. Ex. *Haminea solitaria*: Atlantic coast, Massachusetts to South Carolina.

Family 2. CAVOLINIIDÆ (Fig. 244, b). — Shell present; gill absent; two large epipodia (fins, hence pteropods); pelagic. Ex. *Cavolinia trispinosa*: shell with three long spines; Atlantic coast.

Family 3. APLYSIIDÆ. — Sea Hares. Shell internal, rudimentary; body slug-like; epipodia over back; brightly colored; cosmopolitan. Ex. *Aplysia protea*: 16 cm. long; Florida and West Indies.

Family 4. CLIONIDÆ. — Shell and mantle absent; gill absent; foot modified as a pair of fins; proboscis usually with suckers; pelagic. Ex. *Clione limacina*: Arctic Ocean south to New York; sometimes in enormous schools which color sea; serve as food for whales.

Suborder 2. NUDIBRANCHIA. — Sea Slugs. Shell absent; gills present or absent.

Family 1. DENDRONOTIDÆ. — Body long; tentacles branched; cerata (modified gills) branched in two rows on back. Ex. *Dendronotus arborens* (Fig. 244, c): length, 8 cm.; about 6 transparent cerata in each row; Rhode Island northward.

Family 2. DORIDIDÆ. — Integument with spicules; mantle large; gills retractile; cosmopolitan. Ex. *Doris repanda*: gills in star-shaped group; body covered with small white tubercles; Cape Cod northward.

Family 3. ÆOLIDIDÆ. — No mantle; no spicules in integument; cerata in transverse rows along body; nematocysts in cerata from hydroids used as food. Ex. *Æolis papillosa* (Fig. 244, d): 10 or 12 cerata in a row and 12 to 20 rows on each side; two pairs of cylindrical tentacles; Rhode Island northward.

Family 4. ELYSIIDÆ. — No cerata; body ciliated. Ex. *Elysia chlorotica*: 40 mm. long; bright green with white and red spots; Massachusetts to New Jersey.

Order 3. PULMONATA. — Fresh-Water and Terrestrial Snails. The characteristics of a member of this order have already been described. There are no gills, the mantle cavity serving as a lung; the shell is usually a simple, regular spire, sometimes rudimentary or absent; shell closed by many land snails by temporary epiphragm of calcified slime; one or two pairs of tentacles; hermaphroditic; mostly oviparous, a few viviparous; mostly terrestrial, many in fresh water, a few marine; mostly vegetarian, a few carnivorous; about 20,000 species; two suborders.

Suborder 1. BASOMMATOPHORA. — Mostly in fresh water, a few terrestrial or marine; one pair of tentacles; eyes at base of tentacles; shell usually with conical spire; cosmopolitan.

Family 1. LYMNÆIDÆ. — Spire of shell acute; tentacles flattened. Ex. *Lymnæa stagnalis* (Fig. 243): large, shell with 6 whorls. *Lymnæa palustris*: more than 6 whorls.

Family 2. PHYSIDÆ. — Shell with large lower whorl and acute spire; tentacles filiform; cosmopolitan. Ex. *Physa gyrina* (Fig. 243): shell with five or six whorls; about 22 mm. long; central states. *Physa heterostropha*: shell with four whorls; about 14 mm. long; common in eastern states.

Family 3. PLANORBIDÆ. — Shell discoidal. Ex. *Planorbis trivolvis* (Fig. 243): shell sinistral and with four whorls; North America.

Family 4. ANCYLIDÆ (Fig. 244, e). — Shell conical, non-spiral, with oval aperture. Ex. *Ferrissia parallelus*: river limpet; about 5 mm. long; New England.

**Suborder 2. STYLOMMATOPHORA.** — Terrestrial snails; two pairs of retractile tentacles; eyes at tips of posterior tentacles; shell with conical spire, or rudimentary and concealed, or absent; respiratory pore on right side; cosmopolitan.

Family 1. HELICIDÆ. — Shell with low, conical spire of five to seven whorls. Ex. *Helix pomatia*: French, edible snail. *Polygyra albolabris* (Fig. 244, f): shell with unidentate aperture and closed umbilicus; eastern and central states.

Family 2. ENDODONTIDÆ. — Shell conical or depressed; umbilicus open. Ex. *Anguispira alternata*: shell depressed; gregarious; eastern and Central America. *Helicodiscus parallelus*: shell disk-shaped; diameter about 4 mm.; eastern states.

Family 3. LIMACIDÆ (Fig. 244, g). — Slugs; shell rudimentary, concealed in mouth; nocturnal; habitat moist. Ex. *Limax maximus*: about 16 cm. long; surface of body with tubercles; European species; eastern states and California. *Derocera campestris*: about 25 cm. long; mantle oval; prominent tubercles on dorsal surface; eastern and Central America, California.

Family 4. PHILOMYCIDÆ. — Slugs; shell absent; mantle covering entire dorsal surface. Ex. *Philomycus carolinensis*: about 7 cm. long; eastern and central states.

### 3. CLASS III. SCAPHOPODA

The SCAPHOPODA (Fig. 245) are all marine mollusks of which about twelve genera and three hundred living species are known; nearly three hundred fossil species have also been described. The

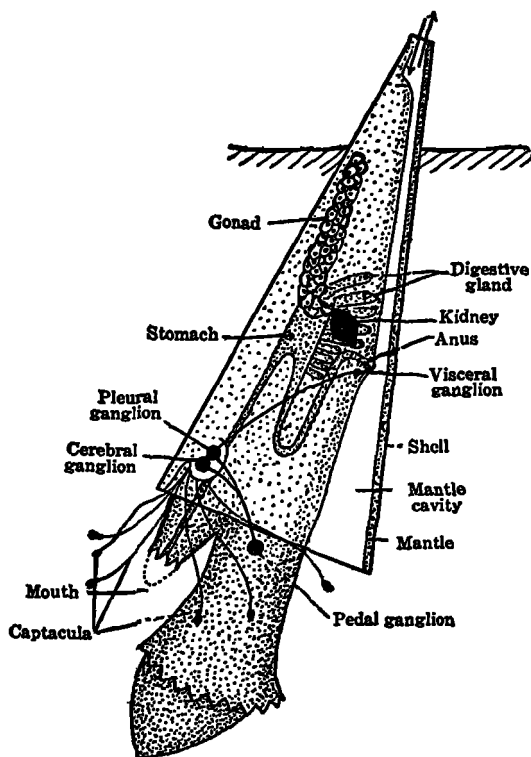


FIG. 245. — SCAPHOPODA. *Dentalium*. Structure of specimen buried in sand except end through which inhalant and exhalant currents of water pass. (After Naef, from Borradaile and Potts, modified.)

body is bilaterally symmetrical and enclosed in a tubular shell open at both ends. The foot is small and used for burrowing. The head is supplied with many tentacles and contains a radula. No gills are present and the circulatory system is rudimentary. Development includes a trochophore larva.

Family 1. DENTALIIDÆ. — Tooth shells; foot trilobate, with two lateral epipodial lobes. Ex. *Dentalium entale*: about 5 cm. long and 5 mm. broad; Cape Cod northward.

Family 2. SIPHONODENTALIIDÆ. — Foot elongate, vermiform. Ex. *Siphonodentalium lobatum*: about 10 mm. long; New England northward.

#### 4. CLASS IV. CEPHALOPODA

##### (1) *LOLIGO PEALII* — A SQUID

*Loligo pealii* (Plate III) is one of the common squids found along the eastern coast of North America from Maine to South Carolina. It probably lives in deep water during the winter, but about May 1 it enters shallow water in large schools to lay its eggs. Squids are of some economic importance, since they are used as food by Chinese and Italians, and as bait for line and trawl

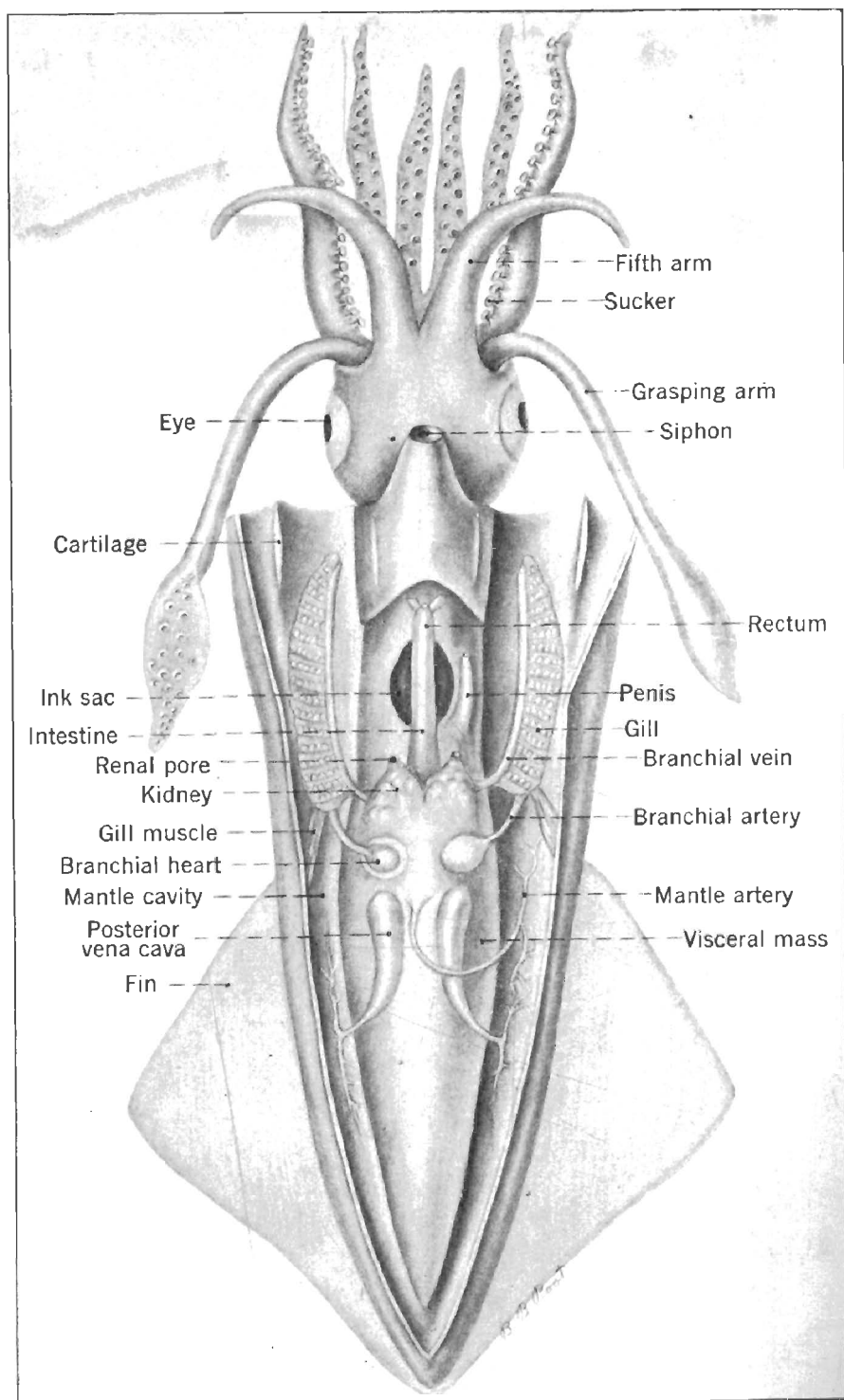


PLATE III. Squid with posterior body wall removed to show internal anatomy.  
(Drawn by Barbara Bradley Root.)

fishings. They feed on small fish, Crustacea, and other squids, and in turn furnish food for cod and other large fish.

**Anatomy and physiology.**—The body of *Loligo* is spindle-shaped. When swimming through the water the morphological ventral surface is usually anterior; the dorsal surface is posterior; the anterior surface is dorsal; and the posterior surface is ventral. The *skin* may change color rapidly; sometimes it is bluish white, at others, mottled red or brown.

The *foot* consists of *ten lobes* and a *funnel*. Eight of the lobes are *arms* and two are long *tentacles*. The inner surfaces of both arms and tentacles are provided with *suckers*. The arms are pressed together and used for steering when the squid swims, but when capturing prey the tentacles are extended, seize the victim with their suckers, and draw it back to the arms, which hold it firmly to the mouth. The *funnel* is a muscular tube extending out beyond the edge of the *mantle collar* beneath the *head*. Water is expelled from the *mantle cavity* through it. The funnel is the principal steering organ; if it is directed forward, the jet of water passed through it propels the animal backward; if directed backward, the animal is propelled forward.

A thick muscular *mantle* encloses the visceral mass and mantle cavity. It terminates ventrally in a *collar* which articulates with the visceral mass and funnel by three pairs of interlocking surfaces. Water is drawn into the mantle cavity at the edge of the collar by the expansion of the mantle and forced out through the funnel by the contraction of the mantle. On each side of the animal is a triangular fin-like projection of the mantle; these *fins* may propel the squid slowly forward or backward by their undulatory movements, or may change the direction of the squid's progress by strong upward or downward strokes.

The *shell* or *pen* of *Loligo* is a feather-shaped plate concealed beneath the skin of the back (anterior surface).

The *true head* is the short region between the arms and the mantle collar; it contains two large *eyes*.

The *digestive system* includes a *pharynx* or buccal mass, *oesophagus*, *salivary glands*, *stomach*, *cecum*, *intestine*, *rectum*, *inksac*, *liver*, and *pancreas*. There are two powerful chitinous *jaws* in the pharynx; they resemble a parrot's beak inverted, and are moved by strong muscles. A *radula* is also present. Two *salivary glands* lie on the dorsal surface of the pharynx, and one is embedded in the ventral

end of the *liver*; they all pour their secretions into the mouth. The *oesophagus* leads from the *pharynx* through the *liver* and into the *stomach*. Closely connected with the muscular *stomach* is the large, thin-walled *cecum*. Food is probably partially digested

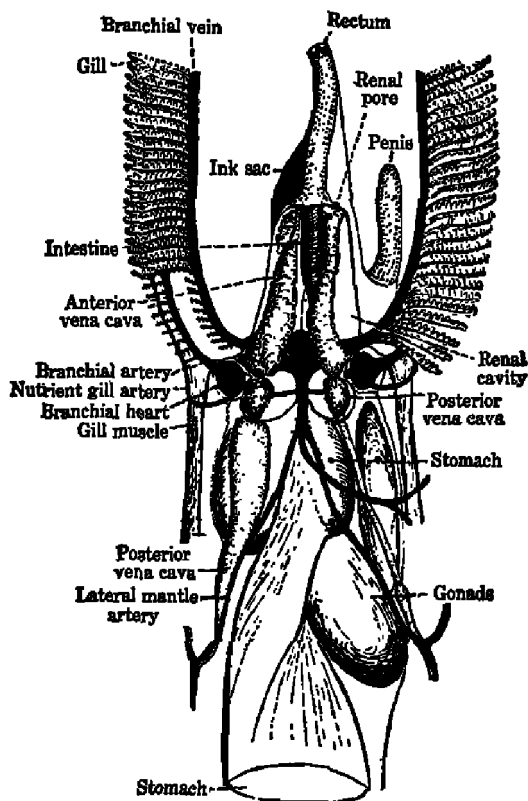


FIG. 246A. — *Loligo pealii*, male. Dissection revealing the circulatory and renal organs. (From Brooks, modified.)

in the *stomach* by fluids brought in from the *pancreas* and *liver*; it then passes into the *cecum*, where digestion is completed and absorption takes place. Bones and other indigestible material are forced from the *stomach* into the *intestine* and out through the *anus*.

The *blood* of the squid is contained in a double, closed vascular



system (Fig. 246, A). Arterial blood is forced by a muscular *systematic heart* to all parts of the body by three *aortæ*: (1) anterior, (2) posterior, and (3) genital. It passes from *arterial capillaries* into *venous capillaries*, and thence into the large *veins*. From these it enters the right and left *branchial hearts*, and is then forced into the *gills* through the *branchial arteries*. In the gills the blood

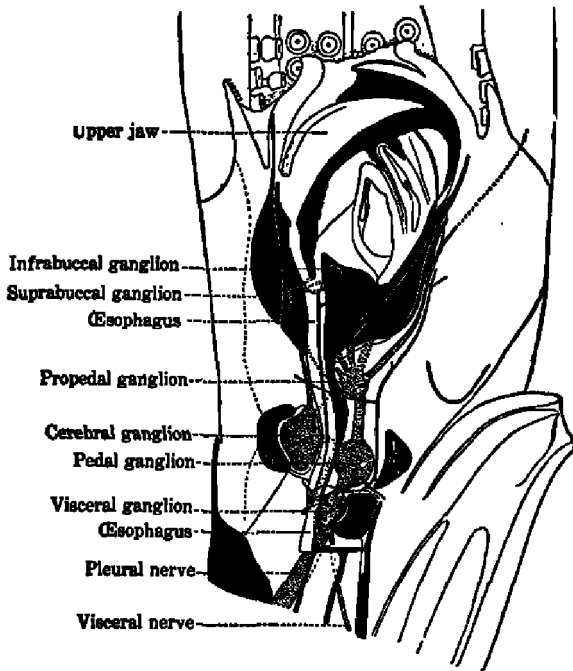


FIG. 246B. — *Loligo pealii*. Longitudinal section through the head showing ganglia and cartilages. (After Williams, from Petrunkevitch.)

is aerated, and is finally carried by the *branchial veins* back to the systemic heart.

There are two *gills* in the squid (Plate III, Fig. 246, A). The water which enters the mantle cavity flows over them, supplying oxygen to the blood and carrying away carbon dioxide.

The two *nephridia* or *kidneys* (Fig. 246, A) are white triangular bodies extending forward from the region of the branchial hearts and opening on either side of the intestine at the ends of small papillæ.

The *nervous system* (Fig. 246, *B*) consists of a number of *ganglia* mostly in the head. The principal ones are the cerebral, pedal, visceral, suprabuccal, infrabuccal, stellate, and optic ganglia.

The *sensory organs* are two very highly developed *eyes*, two *statocysts*, and probably an *olfactory organ*. The *statocysts* are

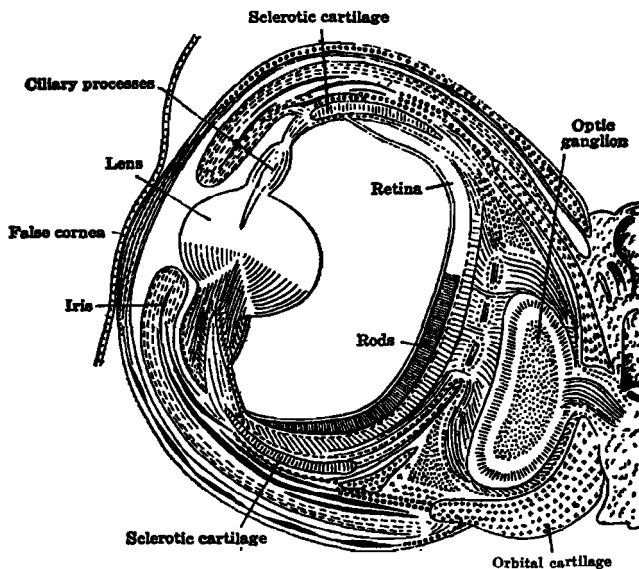


FIG. 247. — Section through the eye of a cephalopod.  
(After Hensen, from Parker and Haswell.)

two vesicles lying side by side in the head; each contains a concretion, the *statolith*, and is probably an organ of equilibrium. The *eyes* (Fig. 247) are large and somewhat similar superficially to those of vertebrates. Just behind the eye is a fold which projects backward under the collar, and is probably olfactory.

Squids are either male or female. The *reproductive organs* (Fig. 246, *A*) of the *male* are the *testis*, a *vas deferens*, a *spermatophoric sac*, which contains sperms bound together into bundles called *spermatophores*, and a copulatory organ, the *penis*. The *female organs* are an *ovary*, *oviduct*, *oviducal gland*, and *nidamental gland*.

## (2) OTHER CEPHALOPODA

The cephalopods are marine mollusks known as squids, devil-fish, cuttlefish, octopods, and nautili. About 150 genera contain

living representatives; most of the species in the class are known only as fossils. The most striking differences between cephalopods and other mollusks are their ability to move about rapidly and their aggressive, carnivorous habits. The body is bilaterally symmetrical. The head is well developed and contains a radula and large, often complex, eyes. Part of the foot has grown around the head and gives rise to mobile, prehensile tentacles, and the other part forms the muscular funnel, or siphon through which

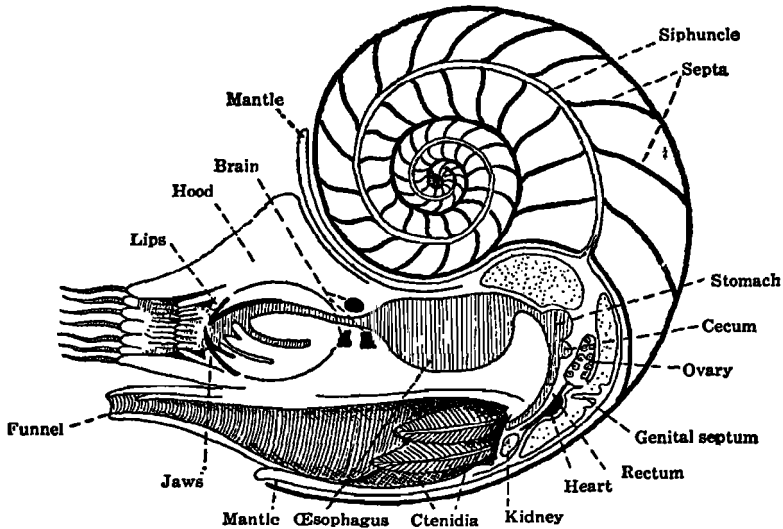


FIG. 248. — *Nautilus pompilius*. Dissection of the "pearly nautilus" showing chambered shell and anatomy of the animal. (From Borradaile and Potts.)

water is expelled from the mantle cavity. The mouth lies in the midst of the tentacles. One or two pairs of gills are present in the mantle cavity. The typical cephalopod possesses a chambered shell and lives in the last and largest, chamber, but most of the living representatives are either without a shell or have one that is reduced and internal. Certain species of squids possess luminous organs that contain symbiotic, luminous bacteria; these are not transmitted from mother to offspring but enter the organs from outside in each generation. The two orders, two suborders, and several of the families are characterized as follows.

**Order 1. TETRABRANCHIA** (Figs. 248, 249, *c*, *d*). — Calcareous shell, closely coiled; tentacles numerous and without suckers;

eyes simple; no chromatophores; no inksac; two pairs of gills and two pairs of nephridia. The only family that contains living representatives is the NAUTILIDÆ with one genus. Ex. *Nautilus*

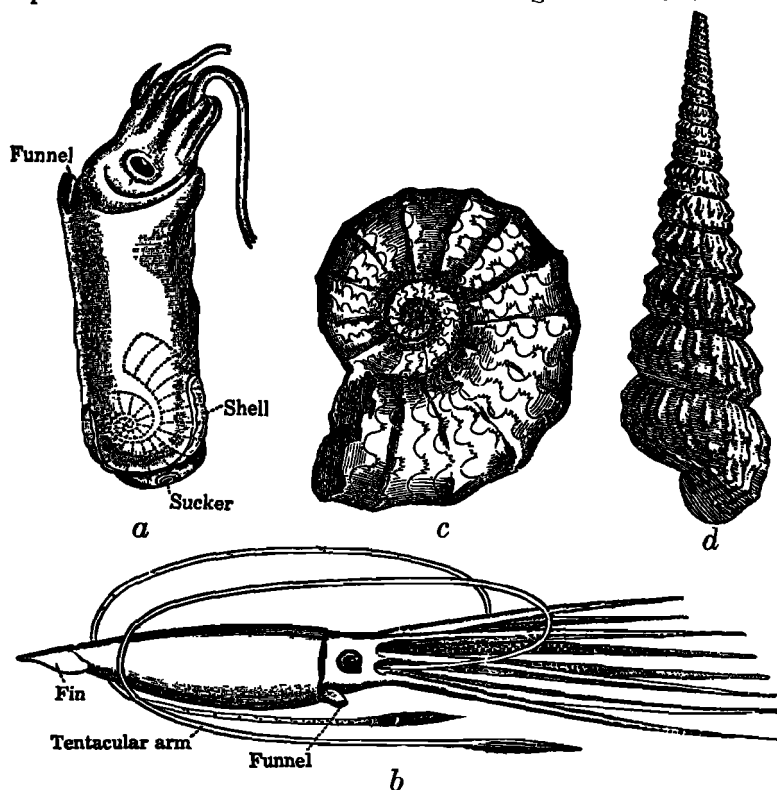


FIG. 249. — CEPHALOPODA: living and fossil types. a, DECAPODA. *Spirula peronii*, a living species containing a spiral, chambered shell almost completely covered by the mantle. b, DECAPODA. *Architeuthis princeps*: the largest living invertebrate. c, TETRABRANCHIA. *Ceritites nodosus*, a Triassic ammonite with shell removed so as to reveal the sutures. d, TETRABRANCHIA. *Turritites costatus*, an uncoiled ammonite from the Lower Chalk. (a, after Owen, from Cooke; b, after Verrill; c, d, from Woods.)

*pompilius*: pearly nautilus (Fig. 248); shell coiled in flat spiral; many chambers formed by curved septa; a slender tube, the siphuncle, passes through chambers near center; shell up to 25 cm. in diameter; edible; Pacific and Indian Oceans.

**Order 2. DIBRANCHIA.** — Shell absent or reduced and internal, calcareous or horny, not coiled; one pair of gills; one pair of ne-

phridia; tentacles 8 to 10, with suckers or hooks; eyes complex; chromatophores and inksac present; two suborders.

**Suborder 1. DECAPODA.** — Shell present, chitinous or calcareous, internal, reduced; ten tentacles, one pair long with suckers near distal end, four pairs short with suckers along entire length.

**Family 1. SPIRULIDÆ.** — An exception to other members of order, since shell is partly external and loosely coiled. Ex. *Spirula*



FIG. 250. — OCTOPODA. *Argonauta pacifica*, a paper nautilus, with its egg case. (From Johnson and Snook.)

*peroni* (Fig. 249, a): shell white; 25 mm. in diameter; Caribbean Sea.

**Family 2. SEPIDÆ.** — Shell calcareous; body oval; one pair narrow fins; cosmopolitan. Ex. *Sepia officinalis*: about 20 cm. long; Europe; edible.

**Family 3. SEPIOLIDÆ.** — Shell chitinous, straight (called a pen); body short and broad; fins large, rounded; eyes with cornea. Ex. *Rossia sublevis*: about 46 mm. long; pinkish, spotted; Cape Cod northward.

**Family 4. LOLIGINIDÆ.** — Body long; fins near posterior end; eyes with cornea. Ex. *Loligo pealii*: common squid (p. 348).

**Family 5. OMMASTREPHIDÆ.** — Body long, cylindrical; fins near posterior end; eyes without cornea; cosmopolitan. Ex. *Architeuthis princeps* (Fig. 249, b): giant squid; body up to 6 meters long; total length including arms, over 50 feet; largest living invertebrate; deep sea.

**Suborder 2. OCTOPODA.** — Shell absent (except in *Argonauta*); 8 arms.

**Family 1. ARGONAUTIDÆ** (Fig. 250). — Shell of female thin, spiral, without septa; male small. Ex. *Argonauta argo*: paper nautilus; Atlantic Ocean.

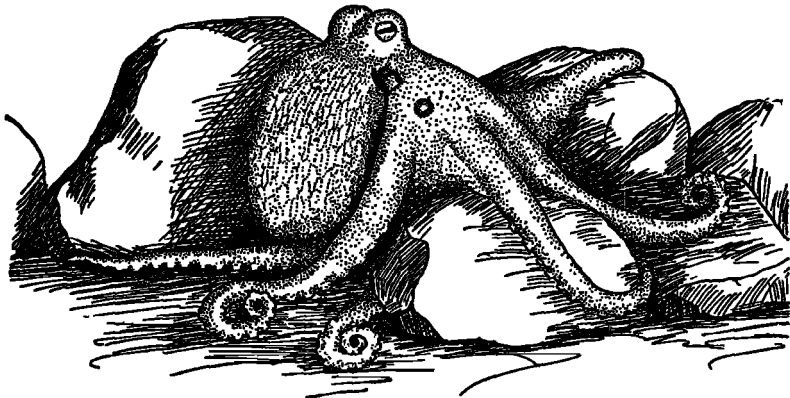


FIG. 251. — OCTOPODA. *Polypus bimaculatus*, an octopus.  
(From Johnson and Snook.)

**Family 2. OCTOPODIDÆ** (Fig. 251). — Devilfishes; body globose; head very large. Ex. *Octopus bairdi*: sea polyp; body about 75 mm. long; arms about 10 cm. long; Cape Cod northward.

## 5. CLASS V. PELECYPODA

### (1) ANODONTA — A FRESH-WATER MUSSEL

**External features** (Fig. 252). — Mussels usually lie almost entirely buried in the muddy or sandy bottom of lakes or streams. They burrow and move from place to place by means of the *foot*, which can be extended from the anterior end of the shell. Water loaded with oxygen and food material is drawn in through a slit-like opening at the posterior end, called the *ventral siphon*, and excretory substances and feces along with deoxygenated water are carried out through a smaller *dorsal siphon*.

**The shell.** — The shell consists of two parts, called *valves*, which are fastened together at the dorsal surface by an elastic ligamentous hinge. In a nearly related genus, *Unio*, the valves articulate with each other by means of projections called teeth, but these

are almost entirely atrophied in *Anodonta*. A number of concentric ridges appear on the outside of each valve; these are called *lines*

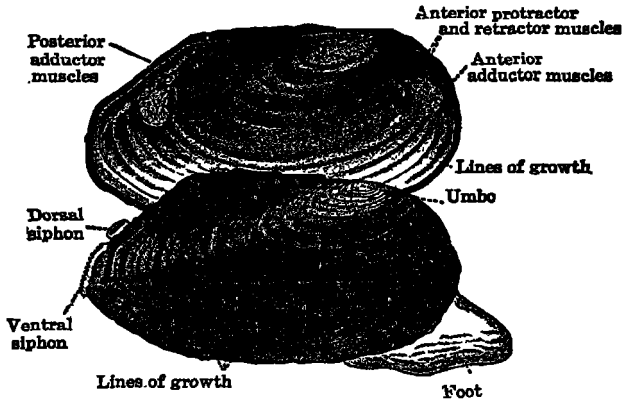


FIG. 252. — *Anodonta*: external features. (From Shipley and MacBride.)

*of growth*, and, as the name implies, represent the intervals of rest between successive periods of growth. The small area situated dorsally toward the anterior end is called the *umbo*; this is

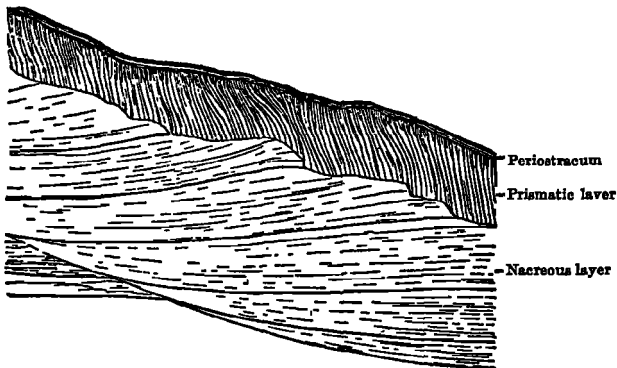


FIG. 253. — *Unio*. Verticle section of shell. (From Woods.)

the part of the shell with which the animal was provided at the beginning of its adult stage. The umbo is usually eroded by the carbonic acid in the water.

The *structure of the shell* is easily determined (Fig. 253). There are three layers: (1) an outer thin, horny layer, the *periostracum*, which is secreted by the edge of the mantle, — it serves to protect

the underlying layers from the carbonic acid in the water, and gives the exterior of the shell most of its color; (2) a middle portion of crystals of carbonate of lime, called the *prismatic layer*, which is also secreted by the edge of the mantle; and (3) an inner *nacreous layer* (mother-of-pearl), which is made up of many thin lamellæ secreted by the entire surface of the mantle, and produces in the light an iridescent sheen.

**Anatomy and physiology** (Plate IV, Fig. 254). — *General account.* — The valves of the shell are held together by two large

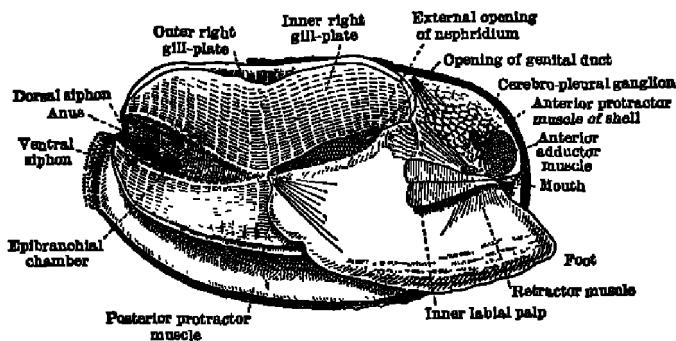


FIG. 254. — *Anodonta mutabilis*, right side, with mantle cut away and right gills folded back. (After Hatachek and Cori, from Shipley and MacBride.)

*transverse muscles* which must be cut in order to gain access to the internal organs. These muscles are situated one close to either end near the dorsal surface; they are called *anterior adductors*, and *posterior adductors*. As the shell grows, they migrate outward from a position near the umbo, as indicated by the faint lines in figure 252. When these muscles are cut, or when the animal dies, the shell gapes open, the valves being forced apart by the elasticity of the *ligamentous dorsal hinge*, which is compressed when the shell is closed.

The two folds of the dorsal wall of the mussel which line the valves are called the *mantle* or *pallium*. The mantle flaps are attached to the inner surface of the shell along a line shown clearly in figure 252. The space between the mantle flaps containing the two pairs of *gill plates*, the *foot*, and the *visceral mass*, is called the *mantle cavity*.

*Digestion.* — The *food* of the mussel consists of organic material carried into the mantle cavity with the water which flows through



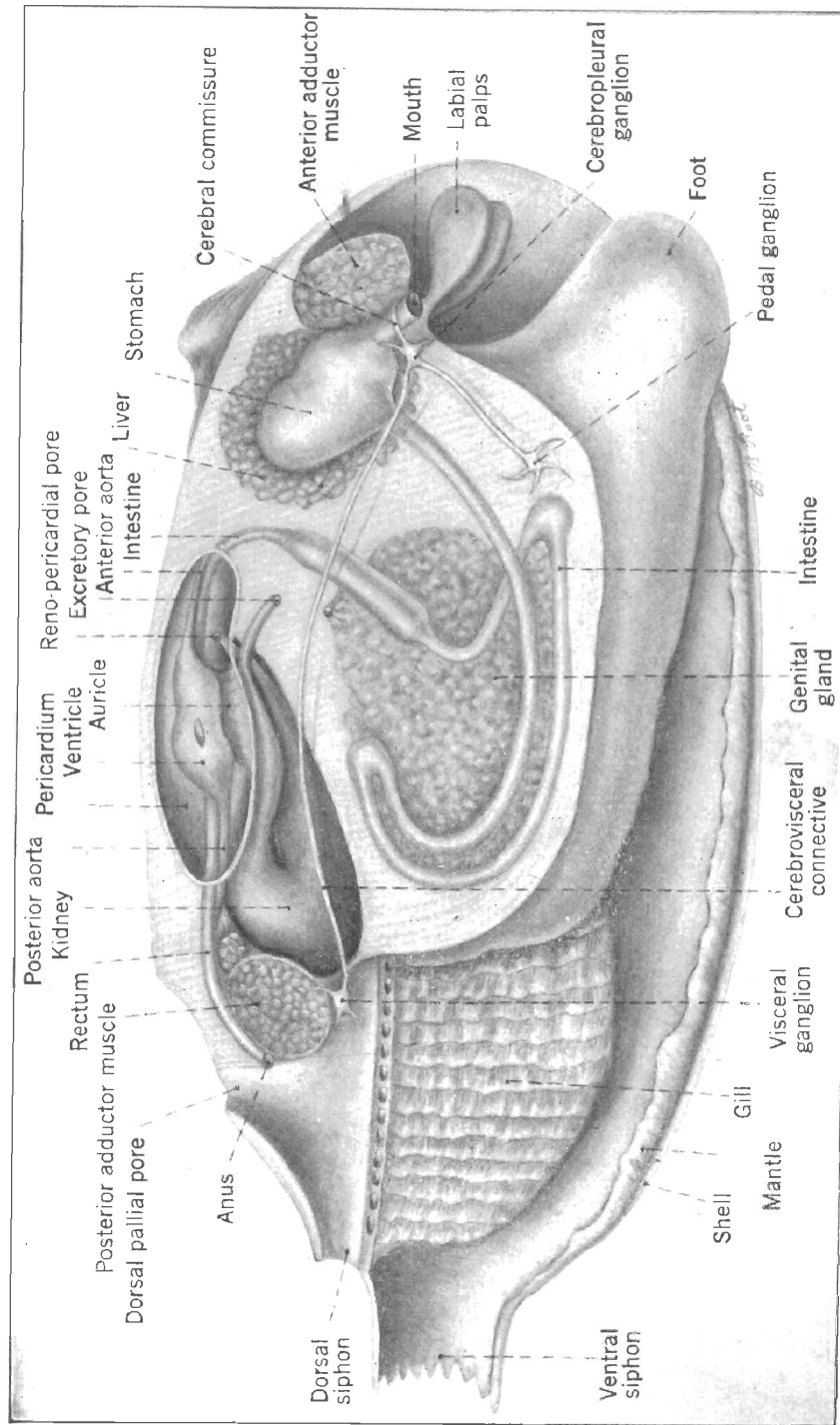


PLATE IV. Longitudinal section of a Fresh-Water Mussel with right gills and part of visceral mass removed to show internal organs. (Drawn by Barbara Bradley Root.)

the ventral siphon. The *mouth* lies between two pairs of triangular flaps, called *labial palps*. The *cilia* (Fig. 257, *b*) on these palps drive the food particles into the mouth. A short *oesophagus* leads from the mouth to the *stomach*. On either side of the stomach is a lobe of a glandular mass called the *digestive gland* or *liver*; a digestive fluid is secreted by the liver and is carried into the stomach by ducts, one for each lobe.

The food is mostly digested and partly absorbed in the stomach; it then passes into the *intestine*, by whose walls it is chiefly absorbed. The intestine coils about in the basal portion of the foot, then passes through the *pericardium*, runs over the posterior adductor muscle, and ends in an *anal papilla*. The faeces pass out of the anus and are carried away by the current of water flowing through the dorsal siphon.

*Circulation.* — The circulatory system comprises a heart, blood vessels, and spaces called sinuses. The *heart* (Plate IV) lies in the *pericardium*. It consists of a *ventricle*,

which surrounds part of the intestine, and a pair of *auricles*. The ventricle, by its contractions drives the blood forward through the *anterior aorta* and backward through the *posterior aorta*. Part of the blood passes into the mantle, where it is oxygenated, and then returns directly to the heart. The rest of the blood circulates

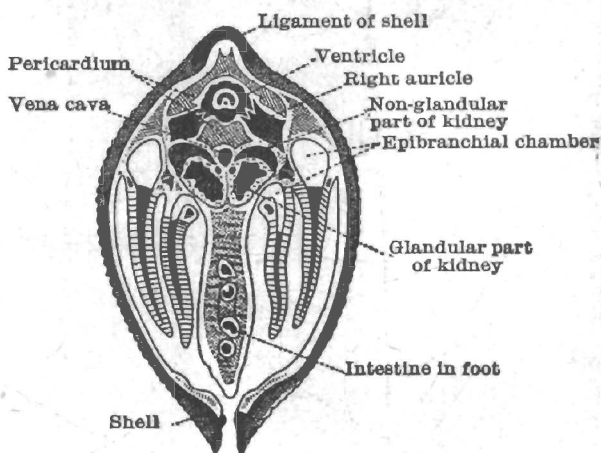


FIG. 255. — *Anodonta*. Diagrammatic section showing especially the gills hanging down into the mantle cavity. (After Howes, from Shipley and MacBride.)

through numerous spaces in the body and is finally collected by a vessel called the *vena cava*, which lies just beneath the pericardium. From here the blood passes into the kidneys, then into the *gills*, and finally through the auricles and into the ventricle. Nutrient and oxygen are carried by the blood to all parts of the body, and carbon dioxide and other waste products of metabolism are transported to the gills and kidneys.

*Respiration.* — The respiratory organs of the mussel are the *gills* or *branchiæ* or *ctenidia*. A pair of these hang down into the mantle cavity on either side of the foot (Fig. 255).

Each *gill* is made up of two plates or lamellæ (Fig. 256) which lie side by side and are united at the edges except dorsally. The cavity between the lamellæ is divided into vertical *water tubes* by partitions called *interlamellar junctions*. Each lamella consists of

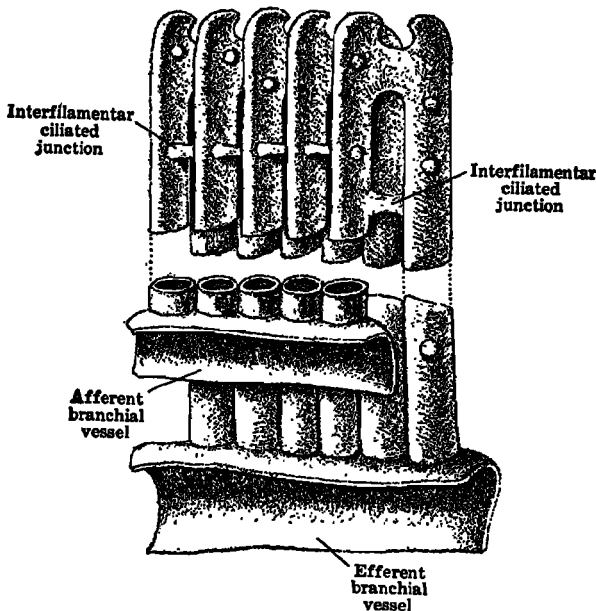


FIG. 256. — *Mytilus*. Diagram of a portion of the gill.  
(From Lankester's Treatise.)

a large number of *gill filaments*, each supported by two *chitinous rods*, and covered with *cilia*. Openings, called *ostia*, lie between the gill filaments, and blood vessels are present in the interlamellar junctions and filaments.

Water is drawn through the *ostia* into the water tubes by the cilia which cover the gill filaments; it flows dorsally into the *epibranchial chamber* (Fig. 255); from here it enters the dorsal mantle cavity and passes out through the dorsal siphon. The blood which circulates through the gills discharges carbon dioxide into the water and takes oxygen from it. Respiration also takes place through the surface of the mantle.

*Excretion.* — The organs of excretion are two U-shaped *kidneys* or *nephridia* lying just beneath the pericardium, one on either side of the vena cava (Plate IV). Each kidney consists of a ventral glandular portion into which the pericardium opens by a ciliated

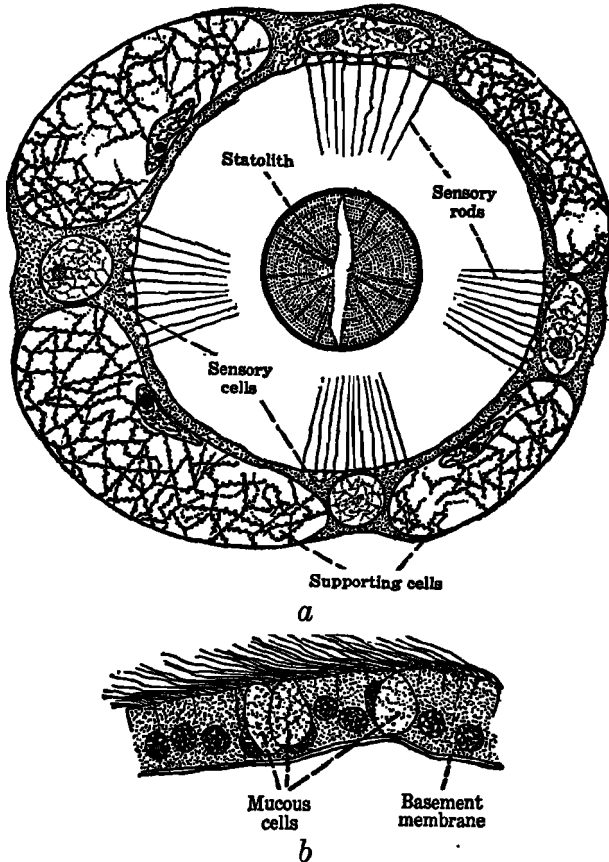


FIG. 257. — a, Statocyst of *Sphaerium*. b, Ciliated epithelium of *Mya*.  
(From Dahlgren and Kepner.)

slit and a dorsal thin-walled bladder which opens to the exterior through the *renal aperture*. Some excretory matter is probably driven into the kidney from the pericardium by cilia, and other excretory matter is taken from the blood by the glandular portion. These waste products of metabolism are carried out of the body through the dorsal siphon.

**Nervous system.** — There are only a few ganglia in the body of the mussel. On each side of the oesophagus is a so-called *cerebropleural ganglion* (Plate IV), connected with its fellow by a nerve called the *cerebral commissure* which passes above the oesophagus. From each cerebropleural ganglion a nerve cord passes ventrally, ending in a *pedal ganglion* in the foot. The two pedal ganglia are closely joined together. Each cerebropleural ganglion also gives off a *cerebrovisceral connective* which may be enclosed by the kidneys and leads to a *visceral ganglion*.

**Sensory organs.** — Fresh-water mussels are not well provided with sensory organs. A small vesicle, the *statocyst*, containing a

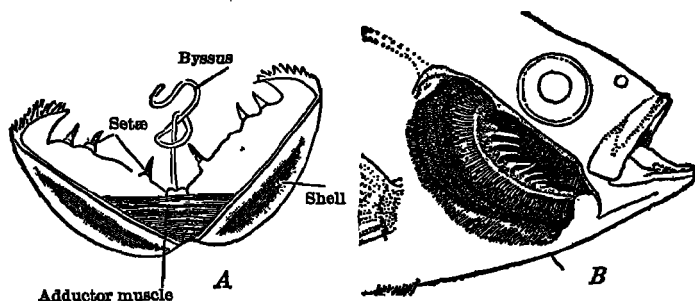


FIG. 258. — A, a young mussel or glochidium. B, the gills of a fish in which are embedded many young mussels forming "blackheads." (A, after Balfour; B, after Lefever and Curtis.)

calcareous concretion, the *statolith*, lies a short way behind the pedal ganglia. It is an organ of equilibrium (Fig. 257, a). A thick patch of yellow epithelial cells covers each visceral ganglion and is known as an *osphradium*. The functions of the osphradia are not certain. They probably test the water which enters the mantle cavity. The edges of the mantle are provided with *sensory cells*; these are especially abundant on the ventral siphon, and are probably sensitive to contact and light.

**Reproduction.** — Mussels are usually either male or female; a few are hermaphroditic. The *reproductive organs* are situated in the foot (Plate IV). They are paired bunches of tubes and open just in front of the renal aperture on each side. The *spermatozoa* are carried out through the dorsal siphon of the male and in through the ventral siphon of the female. The eggs pass out of the genital aperture and come to lie in various parts of the gills according to the species. The spermatozoa enter the gill of the female with the

water and fertilize the eggs. That portion of the gill in which the eggs develop is termed the *marsupium*.

The eggs undergo complete but unequal segmentation. Blastula and gastrula stages are passed through, and then a peculiar larva known as a *glochidium* is produced (Fig. 258). The glochidium has a shell consisting of two valves which are hooked in some species; these may be closed by a muscle when a proper stimulus is applied. A long, sticky thread called the *byssus* extends out from the center of the larva, and bunches of *setæ* are also present.

In *Anodonta* the eggs are fertilized usually in August, and the glochidia which develop from them remain in the gills of the mother all winter. In the following spring they are discharged, and, if they chance to come in contact with the external parts of a fish, this *contact stimulus* causes them to seize hold of it by closing the valves of their shell. The valves cut through the soft tissues of the host, but merely clasp the firmer, deeper organs, such as blood vessels and fin rays. Cells of the host lying near the glochidium migrate toward and completely enclose the partly buried organism. The glochidium probably chemically stimulates the skin of the fish to grow around it, forming the well-known "worms" or "blackheads." While thus embedded the glochidium undergoes a stage of development (metamorphosis), during which the foot, muscles, and other parts of the adult are formed. The glochidium is nourished by tissue severed from the host at the time of attachment, and by the disintegrated larval muscle and larval mantle. Other nutriment consists of transuding tissue juices absorbed from the host. After a *parasitic life* within the tissues of the fish of from three to twelve weeks the young mussel is liberated and takes up a free existence. The liberation of the glochidium is due largely to its own efforts. The injured host tissue is rapidly repaired. Some fishes possess a natural, or racial immunity to infestation with glochidia; others are known to acquire immunity. In the former, many glochidia are destroyed by cytolysis and invasion of the cells of the host. In both cases glochidia are shed, prematurely, at about the second day.

In *Unio* the eggs are fertilized during the late spring and summer, and the glochidia are discharged before the middle of September. The glochidium of *Unio* is smaller than that of *Anodonta* and is usually hookless. It does not as a rule become permanently at-

tached to the fins, operculum, or mouth as in *Anodonta*, but usually lodges on the gill filaments of the fish.

One result of the parasitic habit of larval mussels is the *dispersal of the species* through the migrations of the fish. Only in this way can we account for the rapid colonization of certain streams by mussels, since the adult plows its way through the muddy bottom very slowly.

## (2) OTHER PELECYPODA

This class, for which the term LAMELLIBRANCHIA is also used, contains the bivalve mollusks, such as the clams, mussels, oysters,

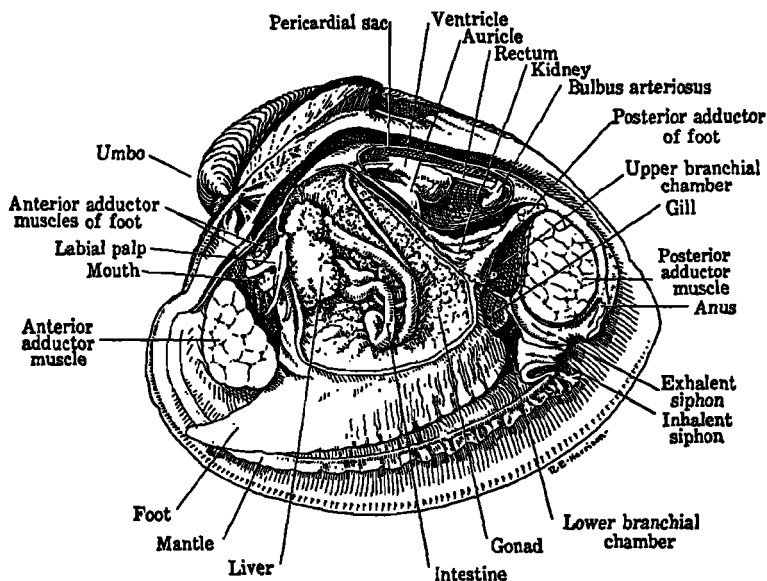


FIG. 259. — *Venus mercenaria*, the hard-shell clam or quahog. Dissection showing organs revealed when left valve, mantle and gills are removed. (From Woodruff.)

scallops, cockles, and ship worms. About four fifths of the more than ten thousand species are marine; the rest live in fresh water. The body is typically bilaterally symmetrical, compressed laterally, and completely covered by a bilobed mantle. The mantle secretes the shell which consists usually of two valves hinged together dorsally and separated ventrally. The head is absent as well as eyes, tentacles, and radula. The foot is usually wedge-

shaped and adapted for burrowing. There are usually two gills on either side of the mantle cavity; these are covered with cilia which help carry minute particles of food to the mouth as well as create a current of fresh water through the mantle cavity. The sexes are usually separate and there are trophophore and veliger larval stages in marine species. The PELECYPODA usually are divided into orders according to the characteristics of their gills. The mussel used as an example of the class has served to

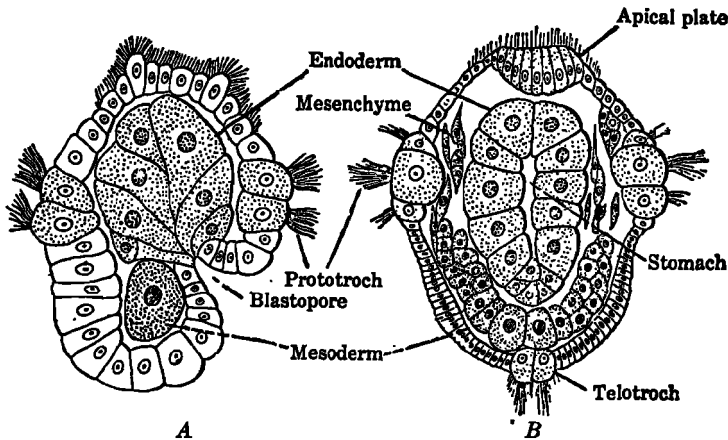


FIG. 260. — *Patella caerulea*. Sections of young larvæ. A, Sagittal section of early stage. B, Frontal section of veliger larva. (After Patten.)

illustrate many of their characteristics; variations from this are indicated in the following account of the orders and a few of the families.

**Order 1. PROTOBRANCHIA.** — Marine. The gills are not lamellar but consist of two rows of short, flat leaflets projecting into the mantle cavity; the foot has a creeping surface with sometimes a fringed margin.

**Family 1. NUCULIDÆ.** — Valves of shell equal in size, oval or triangular; hinge with many teeth; oral palps large; cosmopolitan. Ex. *Nucula proxima*: shell 10 mm. long; in shallow water; South Carolina northward. *Yoldia limatula*: shell about 5 cm. long; North Carolina northward, Pacific coast, Europe.

**Family 2. SOLEMYDÆ.** — Valves of shell equal in size, long, semi-cylindrical, open at ends; foot long and slender; oral palps long. Ex. *Solemya velum*: about 25 mm. long; North Carolina northward.



**Order 2. FILIBRANCHIA.** — Marine. The gills consist of two rows of long filamentous leaflets hanging down into the mantle cavity on either side; the two lamellæ of each gill are usually not joined by partitions; the foot is poorly developed; a byssus is present consisting of tough strings secreted by the foot and of use for purposes of attachment.

Family 1. **ARCIDÆ** (Fig. 261, *a*). — Shell oval, with radial corrugations; valves equal. Ex. *Arca perata*: shell thick; umbo directed obliquely forward; about 35 corrugations; Florida northward.

Family 2. **MYTILIDÆ.** — Mussels; valves equal, long; umbo near or at anterior end; foot cylindrical; attached by byssus. Ex. *Mytilus edulis*: edible mussel; umbo at anterior end; North Carolina northward. *Modiolus modiolus*: horse mussel; umbo near anterior end; burrow in gravel; New Jersey northward.

Family 3. **PECTINIDÆ** (Fig. 261, *b*). — Scallops; valves with a wing on either side of umbo, and with radiating ribs; muscle near center of body. Ex. *Pecten irradians*: common scallop; wings large; twenty radiating ribs; Cape Cod southward. *Pecten grandis*: giant scallop; New Jersey northward.

**Order 3. EULAMELLIBRANCHIA.** — Fresh water and marine. The two gills on each side have the filamentous leaflets connected so as to form two lamellæ (p. 359); siphons present; foot large; byssus small or absent. This order contains most of the lamelibranchs.

Family 1. **UNIONIDÆ.** — Fresh-water clams or mussels; shell large; valves equal; umbo anterior to center; eggs usually carried in outer gill of each pair; glochidia develop from eggs; about one thousand species. Ex. *Lampsilis ventricosa*: pocketbook clam; shell used for making buttons. *Anodonta grandis*: central states. *Ellipio dilatatus*: Mississippi Valley, etc. *Amblema costata*: blue foot clam; shell used for making buttons; Mississippi Valley, etc.

Family 2. **SPHÆRIIDÆ** (Fig. 261, *c*). — Fresh-water or brackish water; shell small, oval; foot elongate, flattened; eggs hatch in inner gill of each pair; many species. Ex. *Sphærium occidentale*: umbo median; about 7 mm. long. *Pisidium abditum*: umbo posterior to middle of shell; about 4 mm. long.

Family 3. **MACTRIDÆ** (Fig. 261, *d*). — Marine; shell large, triangular. Ex. *Mactra solidissima*: giant clam; 15 cm. long; edible.

Family 4. **VENERIDÆ.** — Marine; shell thick. Ex. *Venus mer-*

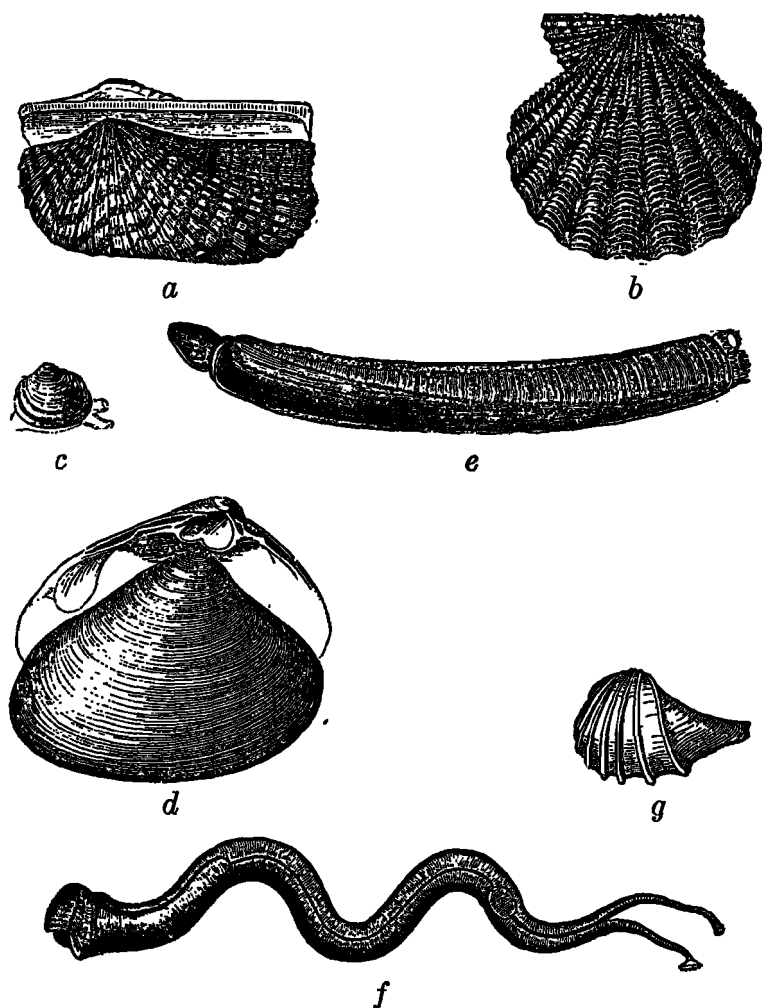


FIG. 261. — PELECYPODA. Types of shells: a-b, FILIBRANCHIA; c-f, EULAMELIBRANCHIA; g, SEPTIBRANCHIA. a, *Arca*. b, *Pecten*. c, *Sphaerium*. d, *Mactra*. e, *Ensis*. f, *Teredo*. g, *Cuspidaria*. (From Tryon.)

*cenaria* (Fig. 259): hard-shell clam or quahog; 11 cm. long; edible; source of wampum of the Indians.

Family 5. MYIDÆ. — Marine; shell not pearly; burrowing habit. Ex. *Mya arenaria*: soft-shell clam; 10 cm. long; edible.

Family 6. SOLENIDÆ (Fig. 261, e). — Marine; shell thin, long narrow; foot large, cylindrical. Ex. *Ensis directus*: razor clam; 15 cm. long and 25 mm. high.

Family 7. TEREDIDÆ (Fig. 261, f). — Marine; vermiform; burrow in wood or clay. Ex. *Teredo navalis*: ship worm; tube about 25 cm. long and 8 mm. in diameter; shell 6 mm. long and 2 mm. broad. At Woods Hole, Massachusetts, *Teredo navalis* breeds from May 10 to October 10. The eggs remain in the mother's gills for about three weeks during cleavage and early larval development. A free-swimming veliger results. The trochophore is non-motile.

Order 4. SEPTIBRANCHIA. — Marine. The gills are absent and a perforated septum divides the mantle cavity horizontally into two chambers.

Family 1. CUSPIDARIIDÆ (Fig. 261, g). — Valves of shell small and almost equal in size; siphons short, fused together. Ex. *Cuspidaria pellucida*: right valve smaller than left, about 12 mm. long; umbo anterior to center; deep water; Massachusetts northward.

## 6. MOLLUSKS IN GENERAL

Interrelations and phylogeny of the Mollusca. — It has been claimed by certain zoologists that the classes of mollusks here recognized do not constitute a homogeneous group; but their internal anatomy is remarkably similar and there is very little doubt of their interrelationship. The AMPHINEURA appear to be the most primitive class in the phylum and to have changed the least from the ancestral condition. The modifications of the other classes have taken place in various directions. The GASTROPODA became a short, creeping type with a spiral, visceral hump revolved through an angle of 180°. The PELECYPODA separated from the rest of the phylum at an early date; they became flattened laterally and developed a large bilobed mantle that secreted a shell of two valves, a large mantle cavity containing gills, and a burrowing foot in place of the creeping type. The CEPHALOPODA have become free-swimming animals, with the foot modified into prehensile tentacles, and with the brain and sense organs highly developed. Two prin-

cipal views exist regarding the relations of the MOLLUSCA to other phyla. One is based largely on anatomy and traces them back to turbellarian-like ancestors. The other, and more probable theory, is based on the presence of trochophore larvæ among both mollusks and annelids, which indicates that these, and other groups that possess a trochophore stage, may be derived from the same ancestral type.

**Embryology.** — Mollusks and annelids correspond remarkably closely in their embryonic development. As in the flatworm, *Planocera* (p. 243), and in representatives of other phyla, a definite cell lineage has been worked out in a number of species. One of the most interesting results obtained is the fact that the quartets that are destined to give rise to definite parts of the embryo and adult have similar values in the flatworms, annelids, and mollusks. There are many variations of a minor type but the first three quartets of micromeres given off by the macromeres form the entire ectoblast of the larva. The first quartet in annelids and mollusks give rise to the pretrochal ectoblast and the second and third to the posttrochal ectoblast. In some cases, as in the TURBELLARIA, the ectoblastic quartets may give rise to mesoblast cells. Three of the macromeres (4A, 4B, and 4C), after three quartets have been given off, are entirely endoblastic; the fourth (4D) is the primary endoblast. It divides into two equal teloblasts from which arise the mesoblastic bands that develop into the coelomic wall and much of the muscular system (Fig. 260).

**The history of our knowledge of the Mollusca.** — Mollusks were well known to the ancients because of their conspicuous shells, and constituted an important article of diet of primitive people. At first the group included a number of types of animals that possessed a superficial resemblance to the mollusks because of their shells, for example, the BRACHIOPODA, TUNICATA, and CIRRIPIEDIA. When the larval stages of the CIRRIPIEDIA were studied it was found that they really belonged to the CRUSTACEA. Investigations of the TUNICATA revealed their chordate nature and vertebrate affinities. Finally the BRACHIOPODA were excluded but placed near the MOLLUSCA in the group MOLLUSCOIDEA. Cuvier (1795) recognized three subdivisions of the MOLLUSCA, (1) GASTROPODA, (2) CEPHALOPODA, and (3) ACEPHALA. They were included by Linnæus as one of the four divisions of the VERMES. Among those who have advanced our knowledge of the

MOLLUSCA in America may be mentioned Ray, Rafinesque, Gould, Simpson, the Binneys, Tryon, and Pilsbry.

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## CHAPTER X

### PHYLUM ARTHROPODA

#### INTRODUCTION

The arthropods comprise the largest phylum in the animal kingdom, surpassing in number of species all the other phyla combined. They may be said to be the dominant animals on the earth at the present time, if numbers of different species and numbers of individuals are accepted as criteria of dominance. To the phylum belong the lobsters, crabs, water fleas,<sup>1</sup> barnacles, millipedes, centipedes, scorpions, spiders, mites, and insects. The most important characteristic common to all of these is the possession of jointed appendages. They are bilaterally symmetrical; consist of a linear series of segments, on all or some of which is a pair of appendages; are covered with a chitinous exoskeleton which is flexible at intervals to provide movable joints; possess a nervous system of the annelid type; have a coelom which is small in the adult, the body cavity being a hæmocœl filled with blood; and are free from cilia.

A brief classification of the phylum is presented below. Subclasses and smaller divisions are given under each class.

CLASS I. CRUSTACEA. Ex. Lobster, crab, barnacle, sow bug.

CLASS II. ONYCHOPHORA. Ex. *Peripatus*.

CLASS III. CHILOPODA. Ex. Centipede.

CLASS IV. DIPLOPODA. Ex. Millipede.

CLASS V. INSECTA. Ex. Grasshopper, honeybee.

CLASS VI. ARACHNOIDEA. Ex. Spider, scorpion, mite.

CLASS VII. PAUROPODA. Ex. *Pauropus*.

CLASS VIII. SYMPHYLA. Ex. *Scutigera*.

#### 1. CLASS I. CRUSTACEA

##### (1) CAMBARUS — A CRAYFISH

Crayfishes inhabit fresh-water lakes, ponds, and streams. The species *Cambarus virilis* is common in some of the central states and *Cambarus affinis* in the eastern part of the country. The

lobster is so nearly like the crayfish in structure that the anatomical portion of this chapter may be applied also in large part to this animal. In Europe the most common crayfish is *Astacus fluvialis*, a species made famous by Huxley's classical work *The Crayfish*.

**External features** (Plate V, Fig. 262). — *Exoskeleton*. — The outside of the body of the crayfish is covered by an extremely

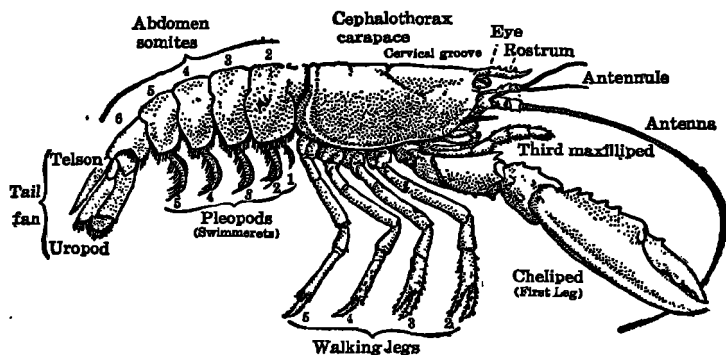


FIG. 262. — External features of a lobster. (After Calman.)

hard chitinous *cuticle* impregnated with lime salts. This exoskeleton is thinner and flexible at the joints, allowing movement.

**Regions of the body.** — The body of the crayfish consists of two distinct regions, an anterior rigid portion, the *cephalothorax*, and a posterior series of segments, the *abdomen*. The entire body is segmented, but the joints have been obliterated on the dorsal surface of the cephalothorax.

**Structure of a segment.** — A typical segment is shown in cross section in figure 265. It consists of a convex dorsal plate, the *tergum*, a ventral transverse bar, the *sternum*, plates projecting down at the sides, the *pleura*, and smaller plates between the pleura and the basis of the limb, the *epimera*.

**Cephalothorax.** — The cephalothorax consists of segments I–XIII, which are enclosed dorsally and laterally by a cuticular shield, the *carapace*. An indentation, termed the *cervical groove*, runs across the mid-dorsal region of the carapace, and obliquely forward on either side, separating the *cephalic* or head region from the posterior *thoracic* portion. The anterior pointed extension of the carapace is known as the *rostrum*. Beneath this on either side is an *eye* at the end of a movable peduncle. The *mouth*

is situated on the ventral surface near the posterior end of the head region. It is partly obscured by the neighboring appendages. The carapace of the thorax is separated by *branchio-cardiac grooves* into three parts, a median dorsal longitudinal strip, the

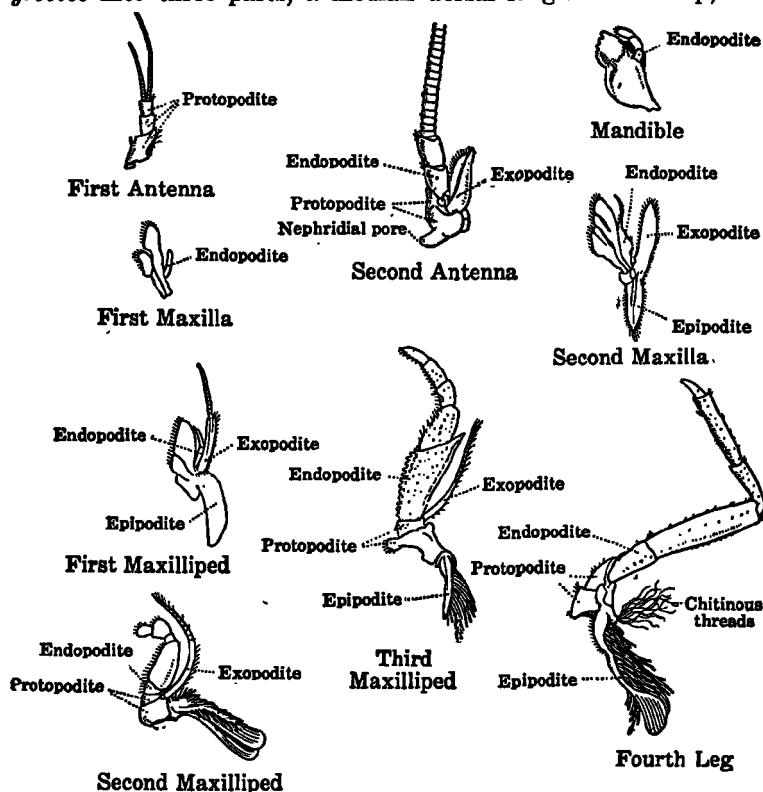


FIG. 263. — Appendages of crayfish as seen from the ventral side. (From Kerr.)

*areola*, and two large convex flaps, one on either side, the *branchio-stegites*, which protect the gills beneath them.

**Abdomen.** — In the abdomen there are six segments, and a terminal extension, the *telson*, bearing on its ventral surface the longitudinal anal opening. Whether or not the telson is a true segment is still in dispute; we shall adopt the view that it is not. The first abdominal segment (XIV) is smaller than the others and lacks the *pleura*. Segments XV–XIX are like the type described above.



**Appendages.** — With the possible exception of the first abdominal segment in the female, every segment of the body bears a pair of jointed appendages. These are all variations of a common type, consisting of a basal segment, the *protopodite*, which bears two branches, an inner *endopodite*, and an outer *exopodite*. Beginning at the anterior end, the appendages are arranged as follows (Fig. 263). In front of the mouth are the *antennules*, and the *antennæ*; the mouth possesses a pair of *mandibles*, behind which are the first, and the second *maxillæ*; the thoracic region bears the first, the second, and the third *maxillipeds*, the *pinchers* or *chelipeds*, and four other pairs of *walking legs*; beneath the abdomen are six pairs of *swimmerets*, some of which are much modified. The accompanying table gives brief descriptions of the different appendages, and shows the modifications due to differences in function. The functions of some of the appendages are still in doubt.

Three kinds of appendages can be distinguished in the adult crayfish; (1) the *foliaceous*, e.g. the second maxilla, (2) the *biramous*, e.g. the swimmerets, and (3) the *uniramous*, e.g. the walking legs. All of these appendages have doubtless been derived from a single type, the modifications being due to the functions performed by them. The biramous type probably represents the condition from which the other types developed. The uniramous walking legs, for example, pass through a biramous stage during their embryological development. Again, the biramous embryonic maxillipeds are converted into the foliaceous type by the expansion of their basal segments.

**General internal anatomy** (Plate V). — The body of the crayfish contains all of the important systems of organs characteristic of the higher animals. The coelom is not a large cavity but is restricted to the cavities of the reproductive organs. Certain of the organs are metamerically arranged, e.g. the *nervous system*; others like the *excretory organs*, are concentrated into a small space. The systems of organs and their functions will be presented in the following order: (1) digestive, (2) vascular, (3) respiratory, (4) excretory, (5) nervous, (6) sense organs, (7) muscular, and (8) reproductive.

**Digestive system.** — The alimentary canal of *Cambarus* consists of the following parts: —

- (1) The *mouth* opens on the ventral surface between the jaws.
- (2) The *oesophagus* is a short tube leading from the mouth to the stomach.

DESCRIPTIVE TABLE OF THE APPENDAGES OF THE CRAYFISH

APPENDAGE	PROTOPODITE	EXOPODITE	ENDOPODITE	FUNCTION
I. Antennule	3 segments; statocyst in basal segment	Many-jointed filament	Many-jointed filament	Tactile; chemical; equilibration
II. Antenna	2 segments; excretory pore in basal segment	Broad, thin, dagger-like lateral projection	A long many-jointed "feeler"	Tactile; chemical
III. Mandible	2 segments; a heavy jaw and basal segment of palp	Absent	Small; 2 distal segments of palp	Crushing food
IV. 1st Maxilla	2 thin lamellæ extending inward	Absent	A small outer lamella	
V. 2d Maxilla	2 bilobed lamellæ	Dorsal half of plate, the scaphognathite	1 segment; small, pointed	Creates current of water in gill chamber
VI. 1st Maxilliped	2 thin segments extending inward; a broad plate, the epipodite extending outward	A long basal segment bearing a many-jointed filament	Small; 2 segments	Chemical; tactile; holds food
VII. 2d Maxilliped	2 segments; a basal coxopodite bearing a gill, and a basipodite bearing the exopodite and endopodite	Similar to VI	5 segments; the basal one long and fused with the basipodite	Similar to VI

DESCRIPTIVE TABLE OF THE APPENDAGES OF THE CRAYFISH (Continued)

APPENDAGE	PROTOPODITE	EXOPODITE	ENDOPODITE	FUNCTION
VIII. 3d Maxilliped	Similar to VII	Similar to VI	Similar to VII, but larger	Similar to VI
IX. 1st Walking Leg (Chela, Cheliped, or Pincher)	2 segments; coxopodite, and basipodite	Absent	5 segments, the terminal two forming a powerful pincher	Offense and defense; aids in walking; tactile
X. 2d Walking Leg (Pereiopod)	Similar to IX	Absent	As in IX, but not so heavy	Walking; prehension; toilet implements
XI. 3d Walking Leg	Similar to IX; coxopodite of female contains genital pore	Absent	Similar to X	Similar to X
XII. 4th Walking Leg	Similar to IX	Absent	Similar to X, but no pincher at end	Walking
XIII. 5th Walking Leg	Similar to IX; coxopodite of male bears genital pore	Absent	Similar to XII	Walking; cleaning abdomen and eggs
XIV. 1st Abdominal (1st Pleopod or Swimmeret)				Reduced in female; in male, protopodite and endopodite fused together forming an organ for transferring sperm

(3) The *stomach* is a large cavity divided by a constriction into an anterior *cardiac* chamber and a smaller posterior *pyloric* chamber. In the stomach are a number of chitinous ossicles of use in chewing the food, and collectively known as the *gastric mill*. The most important of these are (a) a median cardiac ossicle, (b) a median urocardiac ossicle, (c) two lateral pterocardiac ossicles, (d) a pair of lateral zygo-cardiac ossicles, (e) a pyloric ossicle, and (f) a prepyloric ossicle. The ossicles are able to move one upon another, and, being connected with powerful muscles, are effective in grinding up the food. On either side of the pyloric chamber enters a duct of the digestive glands, and above is the opening of the small cecum.

At certain times two calcareous bodies, known as *gastroliths*, are present in the lateral walls of the cardiac chamber of the stomach. Their function is not certain, but is probably the storage of the calcareous matter used in hardening the exoskeleton.

(4) The *intestine* is a small tube passing posteriorly near the dorsal wall of the abdomen, and opening to the outside through the *anus* on the ventral surface of the telson.

The *digestive glands*, or "liver," are situated in the thorax, one on either side. Each consists of three lobes composed of a great number of small tubules. The glandular epithelium lining these tubules produces a secretion which passes into the *hepatic ducts* and thence into the pyloric chamber of the stomach.

**Nutrition.** — *Food.* — The food of the crayfish is made up principally of living animals such as snails, tadpoles, insect larvæ, small fish, and frogs; but decaying organic matter is also eaten. Not infrequently crayfishes prey upon others of their kind. They feed at night, being more active at dusk and daybreak than at any other time. Their method of feeding may be observed in the laboratory if a little fresh meat is offered to them. The maxillipeds and maxillæ hold the food while it is being crushed into small pieces by the mandibles. It then passes through the *œsophagus* into the stomach. The coarser parts are ejected through the mouth.

*Digestion.* — In the cardiac chamber of the stomach, the food is ground up by the ossicles of the gastric mill. When fine enough, it passes through the *strainer* which lies between the two divisions of the stomach. This strainer consists of two lateral and a median ventral fold which bear hair-like *setæ*, and allow the passage of only liquids or very fine particles. In the pyloric chamber, the food

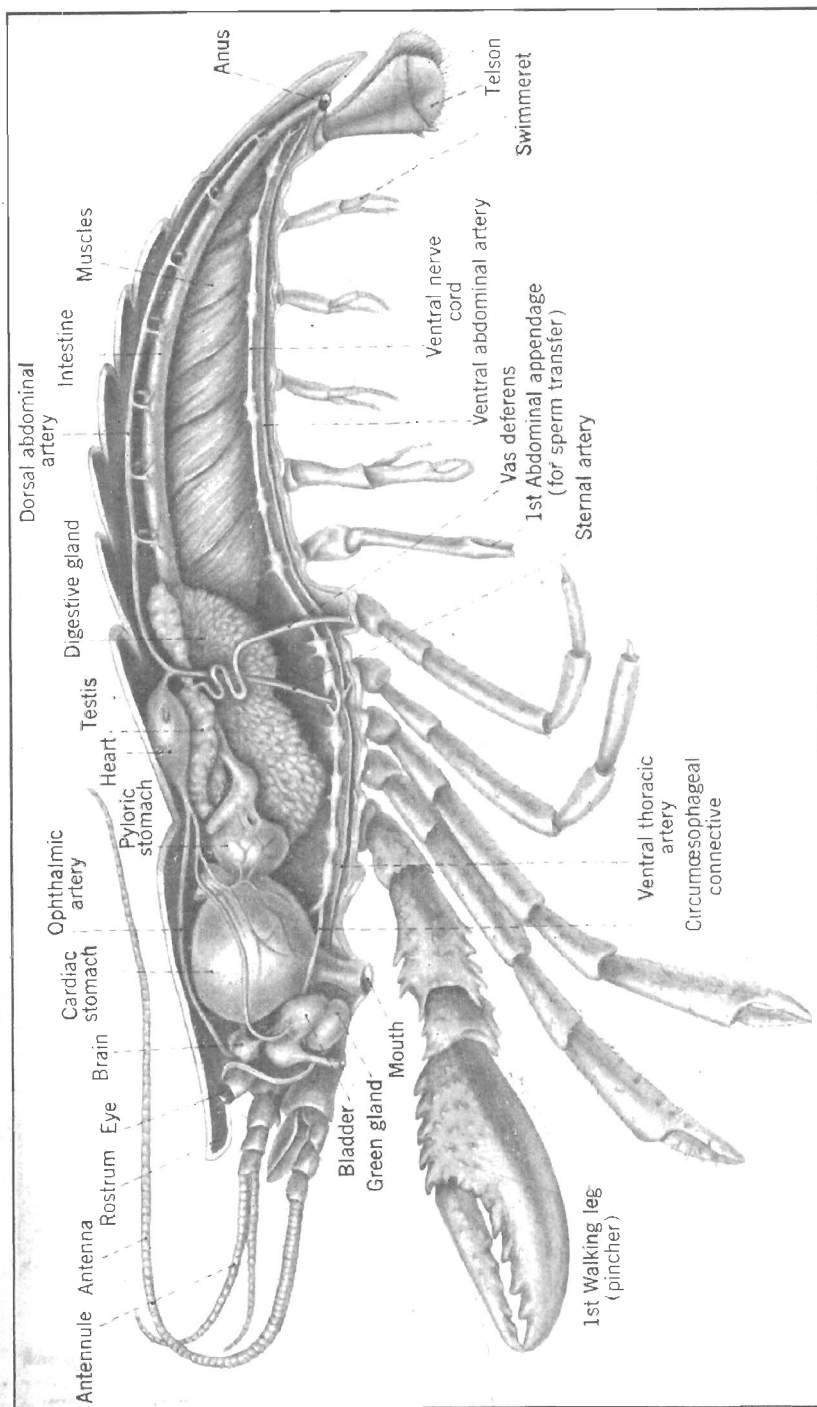


PLATE V. Longitudinal section of a Lobster showing internal organs. (Drawn by Barbara Bradley Root.)

is mixed with the secretion from the digestive glands brought in by way of the hepatic ducts. From the pyloric chamber the dissolved food passes into the intestine by the walls of which the nutritive fluids are absorbed. Undigested particles pass on into the posterior end of the intestine, where they are gathered together into faeces, and egested through the anus.

**Circulatory system.** — *The blood.* — The blood into which the absorbed food passes is an almost colorless liquid in which are suspended a number of amœboid cells, the *blood corpuscles* or amœbocytes. The principal *functions* of the blood are the transportation of food materials from one part of the body to another, of oxygen from the gills to the various tissues, of carbon dioxide to the gills, and of urea to the excretory organs. If a crayfish is wounded, the blood, on coming in contact with the air, thickens,

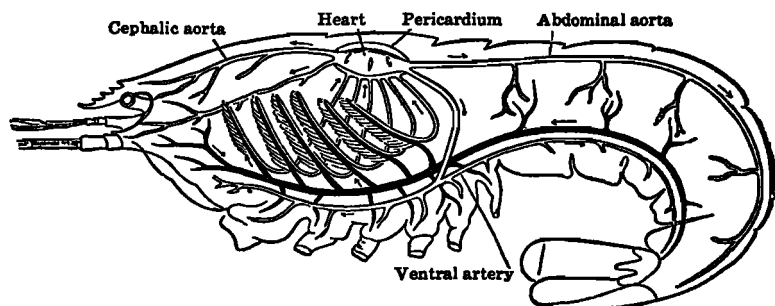


FIG. 264. — Circulatory system of a lobster. (After Gegenbaur.)

forming a clot. It is said to *coagulate*. This clogs the opening and prevents loss of blood. The chelipeds and other walking legs of the crayfish have a breaking point near their bases. When one is injured the animal may break the limb at this point and lessen the blood flow, since only a small space is present in the appendage at this particular spot, and coagulation, therefore, takes place very quickly.

**Blood vessels** (Plate V, Figs. 264, 265). — The principal blood vessels are a heart, seven main arteries, and a number of spaces called sinuses.

**Heart.** — The *heart* is a muscular-walled, saddle-shaped sac lying in the *pericardial sinus* in the median dorsal part of the thorax. It may be considered as a dilatation of a dorsal vessel resembling that of the earthworm. Six elastic *ligaments*, two an-

terior, two posterior, and two running along the ventral border of each lateral surface, fasten it to the walls of the pericardial sinus. Three pairs of valvular apertures, called *ostia*, one dorsal and two lateral, allow the blood to enter from the surrounding sinus.

*Arteries.* — Five arteries arise from the anterior end of the heart.

(1) The *ophthalmic* artery is a median dorsal tube passing forward over the stomach, and supplying the cardiac portion, the oesophagus, and head.

(2, 3) The two *antennary* arteries arise one on each side of the ophthalmic artery, pass forwards, outwards, and downwards, and

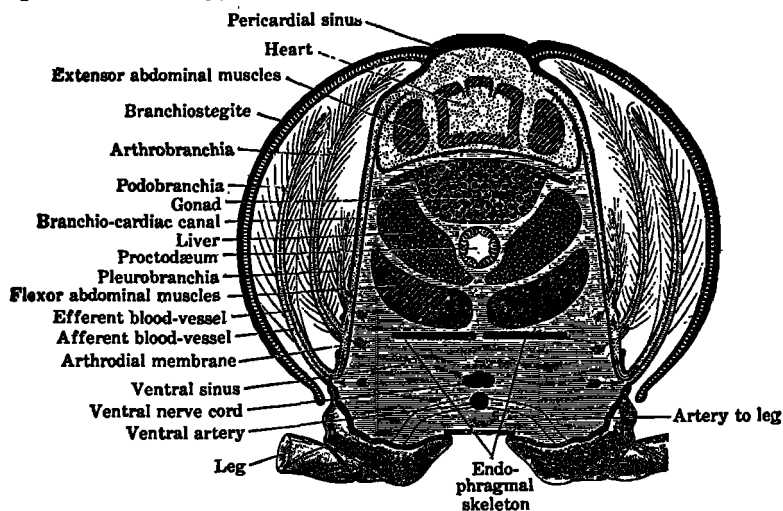


FIG. 265. — Diagrammatic transverse section through the thorax of a crayfish. The dotted spaces contain arterial blood, and the spaces shaded with horizontal lines contain venous blood. The arrows indicate the direction of the blood flow. (From Marshall and Hurst.)

branch, sending a gastric artery to the cardiac part of the stomach, arteries to the antennæ, to the excretory organs, and to the muscles and other cephalic tissues.

(4, 5) The two *hepatic* arteries leave the heart below the antennary arteries. They lead directly to the digestive glands.

A single dorsal abdominal artery arises from the posterior end of the heart.

(6) The *dorsal abdominal artery* is a median tube leading backwards from the ventral part of the heart, and supplying the

dorsal region of the abdomen. It branches near its point of origin, giving rise to the *sternal* artery; this leads directly downward, and, passing between the nerve cords connecting the fourth and fifth pairs of thoracic ganglia (see Plate V) divides into two arteries. One of these, the *ventral thoracic* artery, runs forward beneath the nerve chain, and sends branches to the ventral thoracic region, and to appendages III to XIII; the other, the *ventral abdominal* artery, runs backward beneath the nerve chain, and sends branches to the ventral abdominal region and to the abdominal appendages.

*Sinuses.* — The blood passes from the arteries into spaces lying in the midst of the tissues, called sinuses. The pericardial sinus has already been mentioned. The thorax contains a large ventral blood space, the *sternal sinus*, and a number of *branchio-cardiac canals* extending from the bases of the gills to the pericardial sinus. A *perivisceral sinus* surrounds the alimentary canal in the *cephalothorax*.

*Blood flow* (Fig. 265). — The heart, by means of rhythmical contractions, forces the blood through the arteries to all parts of the body. Valves are present in every artery where it leaves the heart; they prevent the blood from flowing back. The finest branches of these arteries, the *capillaries*, open into spaces between the tissues, and the blood eventually reaches the sternal sinus. From here it passes into the *efferent channels* of the gills and into the gill filaments, where the carbonic acid in solution is exchanged for oxygen from the water in the branchial chambers. It then returns by way of the *afferent gill channels*, passes into the branchio-cardiac sinuses, thence to the pericardial sinus, and finally through the ostia into the heart. The valves of the ostia allow the blood to enter the heart, but prevent it from flowing back into the pericardial sinus.

*Respiratory system* (Fig. 265). — Between the branchiostegites and the body wall are the branchial chambers containing the gills. At the anterior end of the branchial chamber is a channel in which the *scaphognathite* of the second maxilla (Fig. 263) moves back and forth, forcing the water out through the anterior opening. Water flows in through the posterior opening of the branchial chamber.

*Gills.* — There are two rows of gills, named according to their points of attachment. The outermost, the *podobranchiæ*, are fastened to the coxopodites of certain appendages and the inner double



row, the *arthrobranchiæ*, arise from the membranes at the bases of these appendages. In *Astacus* there is a third row, the *pleurobranchiæ*, attached to the walls of the thorax. The number and arrangement of these gills are shown in the accompanying table. The podobranchiæ consist of a basal plate covered with delicate setæ and a central axis bearing a thin, longitudinally folded corrugated plate on its distal end, and a feather-like group of *branchial filaments*. The arthrobranchiæ have a central stem on either side of which extends a number of filaments, causing the entire structure to resemble a plume. Attached to the base of the first maxilliped is a broad thin plate, the *epipodite*, which has lost its branchial filaments.

THE NUMBER AND POSITION OF THE GILLS OF THE CRAYFISH  
(*Cambarus*)

SEGMENT	PODOBRANCHIÆ	ARTHROBRANCHIÆ		TOTAL NUMBER
		<i>Anterior</i>	<i>Posterior</i>	
VI	0 ( <i>ep.</i> )	0	0	0 ( <i>ep.</i> )
VII	1	1	0	2
VIII	1	1	1	3
IX	1	1	1	3
X	1	1	1	3
XI	1	1	1	3
XII	1	1	1	3
	6 ( <i>ep.</i> )	6	5	17 ( <i>ep.</i> )

**Excretory system.** — The excretory organs are a pair of rather large bodies, the "*green glands*" (Plate V), situated in the ventral part of the head anterior to the œsophagus. Each green gland consists of a glandular portion, green in color, a thin-walled dilatation, the bladder, and a duct opening to the exterior through a pore at the top of the papilla on the basal segment of the antenna.

**Nervous system** (Plate V). — The morphology of the nervous system of the crayfish is in many respects similar to that of the earthworm. The *central nervous system* includes a dorsal ganglionic mass, the *brain*, in the head, and two *circum-œsophageal connectives* passing to the *ventral nerve cord*, which lies near the median ventral surface of the body.

**Brain.** — The brain is a compact mass larger than that of the earthworm, and supplies the eyes, antennules, and antennæ with nerves.

*Ventral nerve cord.* — The ganglia and connectives of the ventral nerve cord are more intimately fused than in the earthworm, and it is difficult to make out the double nature of the connectives, except between segments XI and XII, where the sternal artery passes through. Each segment posterior to VII possesses a ganglionic mass, which sends nerves to the surrounding tissues. The large suboesophageal ganglion in segment VII consists of the ganglia of segments III–VII fused together. It sends nerves to the mandibles, maxillæ, and first and second maxillipeds.

The *visceral nervous system* consists of an anterior visceral nerve which arises from the ventral surface of the brain, is joined by a nerve from each circumoesophageal connective, and, passing back, branches upon the dorsal wall of the pyloric part of the stomach, sending a *lateral nerve* on each side to unite with an *infero-lateral nerve* from the *stomatogastric ganglion*.

*Sense organs.* — *Eyes.* — The eyes of the crayfish are situated at the end of movable stalks which extend out, one from each side of the rostrum (Plate V). The external convex surface of the eye is covered by a modified portion of the transparent cuticle, called the *cornea*. This cornea is divided by a large number of fine lines into four-sided areas, termed *facets*. Each facet is but the external part of a long visual rod known as an *ommatidium*.

Sections (Fig. 266) show the compound eye to be made up of similar ommatidia lying side by side, but separated from one another by a layer of dark pigment cells. The average number of ommatidia in a single eye is 2500.

Two ommatidia are shown in figure 267. Beginning at the outer surface, each ommatidium consists of the following parts: (a) a *corneal facet*, (b) two *corneagen* cells which secrete the cornea, (c) a *crystalline cone* formed by four cone cells, or *vitrellæ*, (d) two *retinular cells* surrounding the cone, (e) seven retinular cells which form a *rhabdom* consisting of four *rhabdomeres*, and a number of

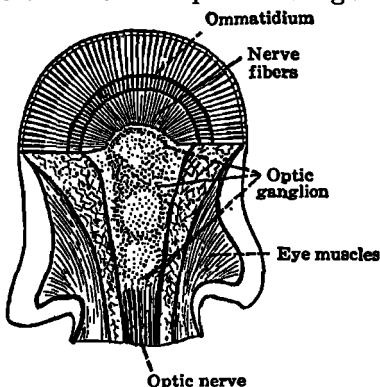


FIG. 266. — Crayfish. Eye in longitudinal section. (After Borradaile and Potts, modified.)

*pigment cells*. Fibers from the *optic nerve* enter at the base of the ommatidium and communicate with the inner ends of the retinular cells.

*Vision*. — The *eyes* of the crayfish are supposed to produce an *erect mosaic* or "*apposition image*"; this is illustrated in figure 268 where the ommatidia are represented by *a-e* and the fibers from the

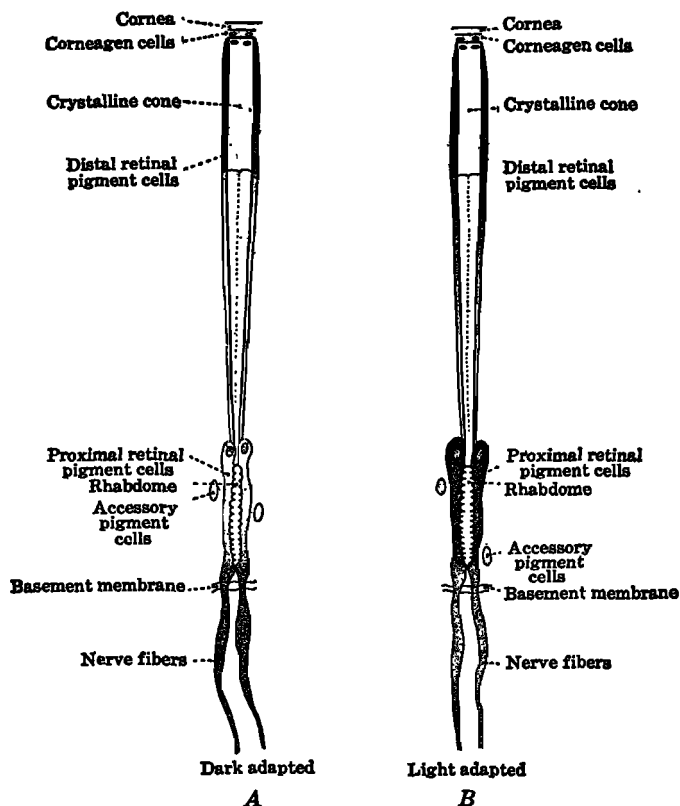


FIG. 267. — *Cambarus virilis*. Longitudinal sections of two ommatidia showing the arrangement of retinal pigment under light adapted and dark adapted conditions. (After Bennitt and Merrick.)

optic nerve by *a'-e'*. The rays of light from any point *a*, *b*, or *c*, will all encounter the dark pigment cells surrounding the ommatidia and be absorbed, except the ray which passes directly through the center of the cornea as *d* or *e*; this ray will penetrate to the retinulae, and thence to the fibers from the optic nerve. "Thus the

retinula of one ommatidium receives a single resultant impression from the light which reaches it. But the adjacent ommatidia being directed to a different, though adjoining, region of the outer world, may transmit a different impression, and the stimuli from all the ommatidia which make up a compound eye will correspond in greater or less degree to the whole of the visible outer world which subtends their several optic axes. The sum of the resulting images which we may thus suppose to be transmitted to the brain may be compared to a mosaic in which the effect is given by a large number of separate pieces of one size and each of uniform colour." (Sedgwick.) This method of image formation is especially well adapted for recording motion, since any change in the position of a large object affects the entire 2500 ommatidia.

When the pigment surrounds the ommatidia (Fig. 267, *B*), vision is as described above; but it has been found that in dim light the pigment migrates partly toward the outer and partly toward the basal end of the ommatidia (Fig. 267, *A*). When this occurs the ommatidia no longer act separately, but a combined image is thrown on the reticular layer. "In this manner an erect '*superposition image*' is formed, the rays refracted by a large number of crystalline cones being superposed at the focus on the retina, and a stimulus far stronger in proportion to the intensity of the illumination than that of the apposition image, though probably much less distinct in detail, is given to the retinulae."

A reflecting pigment is present in the eyes of certain crustaceans which consists of amorphous guanin and forms a reflecting layer below the rhabdomes. This layer increases the efficiency of the eye at low light intensities.

A hormone has been obtained from the eye stalk of many crustaceans that brings about contraction of chromatophores in CRUSTACEA. It produces melanophore expansion in frog tadpoles and melanophore contraction in fishes.

*Statocysts*.—The statocysts of *Cambarus* are chitinous-walled sacs situated one in the basal segment of each antennule. In the

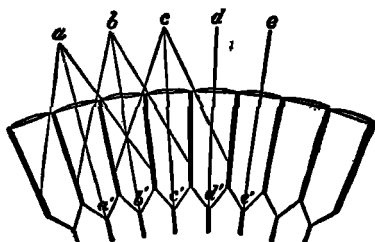


FIG. 268. — Diagram of part of a compound eye which serves to explain mosaic vision. (After Lubbock.)

base of the statocyst is a ridge, called the *sensory cushion*, and three sets of *hairs*, over two hundred in all, each innervated by a single nerve fiber. Among these hairs are a number of large grains of sand, the *statoliths*, which are placed there by the crayfish. Beneath the sensory cushion are *glands* which secrete a substance for the attachment of the statoliths to the hairs.

The statocyst for many years was considered an auditory organ, and it may possibly function as such, though later investigations have proven that it is primarily an organ of *equilibration*. The contact of the statoliths with the statocyst hairs determines the

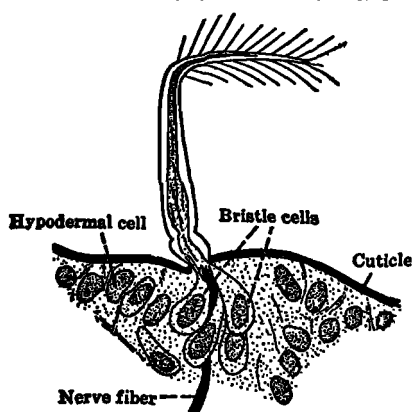


FIG. 269. — Sensory hair from the statocyst of a shrimp, *Palæmonetes*. (After Prentiss; from Dahlgren and Kepner.)

orientation of the body while swimming, since any change in the position of the animal causes a change in the position of the statoliths under the influence of gravity. When the crayfish changes its exoskeleton in the process of molting, the statocyst is also shed. Individuals that have just molted, or have had their statocysts removed, lose much of their powers of orientation. Perhaps the most convincing proof of the function of equilibration is that furnished by

the experiments of Kreidl. This investigator placed shrimps, which had just molted and were therefore without statoliths, in filtered water. When supplied with iron filings, the animals filled their statocysts with them. A strong electro-magnet was then held near the statocyst, and the shrimp took up a position corresponding to the resultant of the two pulls, that of gravity and of the magnet.

**Muscular system.** — The principal muscles in the body of the crayfish are situated in the abdomen, and are used to bend that part of the animal forward upon the ventral surface of the thorax, thus producing backward locomotion in swimming. Other muscles extend the abdomen in preparation for another stroke. Figure 265 shows a cross section of a thoracic segment. The powerful flexor muscles occupy a large part of the space. In the dorsal region are

the less powerful extensor muscles. Other muscles of considerable size are situated within the tubular appendages, especially the chelipeds. A comparison of the skeleton and muscles of the crayfish with those of man is interesting. The skeleton of the crayfish is external and tubular, except in the ventral part of the thorax (Fig. 265). The muscles are internal, and attached to the inner

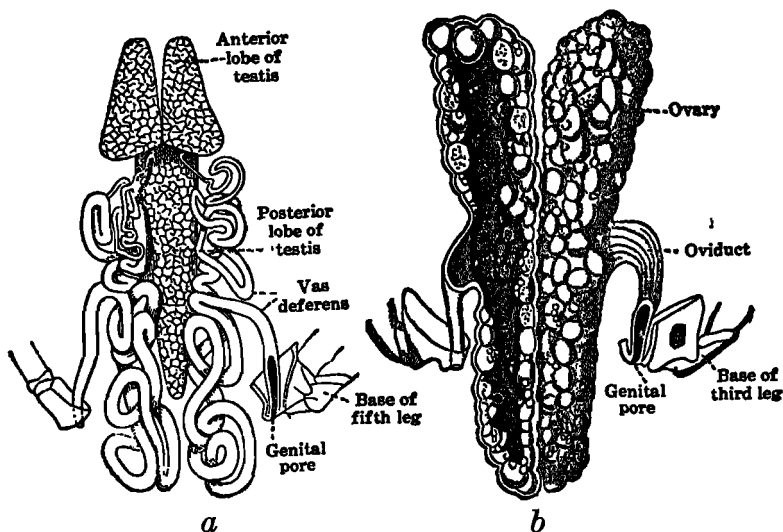


FIG. 270. — Reproductive organs of the crayfish. a, male. b, female. (From Shipley and MacBride.)

surface of the skeleton. In man, on the other hand, the skeleton is internal and the muscles external.

**Reproductive system.** — Crayfishes are normally *diœcious*, there being only a few cases on record where both male and female reproductive organs were found in a single specimen.

**Male reproductive organs.** — The male organs (Fig. 270, a) consist of a *testis* and two *vasa deferentia* which open through the coxopodites of the fifth pair of walking legs. The testis lies just beneath the pericardial sinus (Plate V). It is a soft white body possessing two anterior lobes and a median posterior extension. The *vasa deferentia* are long coiled tubes.

**Spermatogenesis.** — The primitive germ cells within the testis pass through two maturation divisions, and then metamorphose into spermatozoa. These are flattened spheroidal bodies when

enclosed within the testis or vas deferens, but if examined in water or some other liquid they are seen to uncoil, finally becoming star-shaped.

The spermatozoa remain in the testis and vasa deferentia until copulation takes place. As many as two million spermatozoa are contained in the vasa deferentia of a single specimen.

*Female reproductive organs* (Fig. 270, b). — The *ovary* resembles the testis in form, and is similarly located in the body (Fig. 108). A short *oviduct* leads from near the center of each side of the ovary to the external aperture in the coxopodite of the third walking leg.

*Oogenesis*. — The primitive germ cells in the walls of the ovary grow in size, become surrounded by a layer of small cells, the follicle, which eventually break down, allowing the eggs to escape into the central cavity of the ovary. At the time of laying, the ova pass out through the oviduct.

*Breeding habits*. — The details of copulation, egg-laying, and the larval stages of *Cambarus* have been derived from observations of several different species, since the entire life history of a single species has never been recorded. The development of the eggs of *Cambarus* from the time of deposition to the time of hatching has likewise never been investigated.

The principal events in the reproduction of crayfishes may be enumerated as follows: —

(1) Copulation, during which the spermatozoa are transferred from the vasa deferentia of the male to the seminal receptacle of the female; (2) egg-laying; (3) the embryonic development of the eggs; (4) hatching; (5) the growth of the young crayfishes.

*Copulation*. — Copulation in crayfishes, in most cases, takes place in September, October, or November of the first year of their lives, that is, when they are about four months old. A second copulating season is passed through at the end of the second summer, when the animals are about seventeen months old, and a third copulating season occurs at the end of the third summer. At these times a male approaches a female, grasps her by her cephalic appendages, and, after a struggle, turns her over on her back. He then stands over her and transfers spermatozoa to the seminal receptacle. During this process, the spermatozoa flow out of the openings of the vasa deferentia, pass along the grooves on the first abdominal appendages of the male, and enter the seminal

receptacle. Here they are stored during the winter. The *seminal receptacle* is a cavity in a fold of cuticle lying between the sterna of the segments bearing the fourth and fifth pairs of walking legs.

*Egg-laying.* — The eggs are laid at night during the month of April. First the ventral side of the abdomen is thoroughly cleaned of all dirt by the hooks and comb-like bristles near the end of the fifth pair of walking legs. A clear slime or *glair* is secreted by *cement glands* situated chiefly on the basal parts of the uropods, and on the endopodites of the other abdominal appendages. This milky glair gradually covers the swimmerets. The female then lies on her back, and an apron-like film of glair is constructed between the ends of the uropods and telson, and the bases of the second pair of walking legs. The eggs emerge from the openings of the oviducts in the bases of the third pair of walking legs, flow posteriorly, and become attached to the hairs on the swimmerets by strings of a substance no doubt secreted by the cement glands. This is brought about by the turning of the animal first on one side and then on the other a number of times. From one hundred to over six hundred greenish eggs are laid by a single female, depending upon the size and age of the animal. After the eggs are laid the crayfish rights herself, the apron of glair breaks down, and the abdomen is extended.

*Fertilization.* — The method of fertilization has never been discovered. It is supposed that as the eggs are laid they pass over the opening of the seminal receptacle, and are then penetrated by the spermatozoa which were placed there by the male the preceding autumn.

*Embryology.* — While the eggs are developing they are protected by the abdomen of the female, and are *aerated* and kept free from dirt by the waving of the swimmerets back and forth. The embryology of *Cambarus* has never been investigated, but it probably resembles closely the development of the common European crayfish, *Astacus fluviatilis*.

As already noted, the eggs of the crayfish are attached to the swimmerets of the mother by a glutinous secretion. They die if removed, although those of the lobster do not. All of the eggs carried by one crayfish are in the same stage of development at the same time. Embryonic development is slow, several months being required. Most of the egg consists of *yolk* which greatly interferes with cleavage (Fig. 271, A). The *fusion nucleus* lies within



the yolk in a little island of cytoplasm. The nuclei that arise from it migrate to the periphery (B) and the egg then divides into incomplete columnar *blastomeres* called *primary yolk pyramids*, each with a single nucleus at the outer end (C). This *blastula*

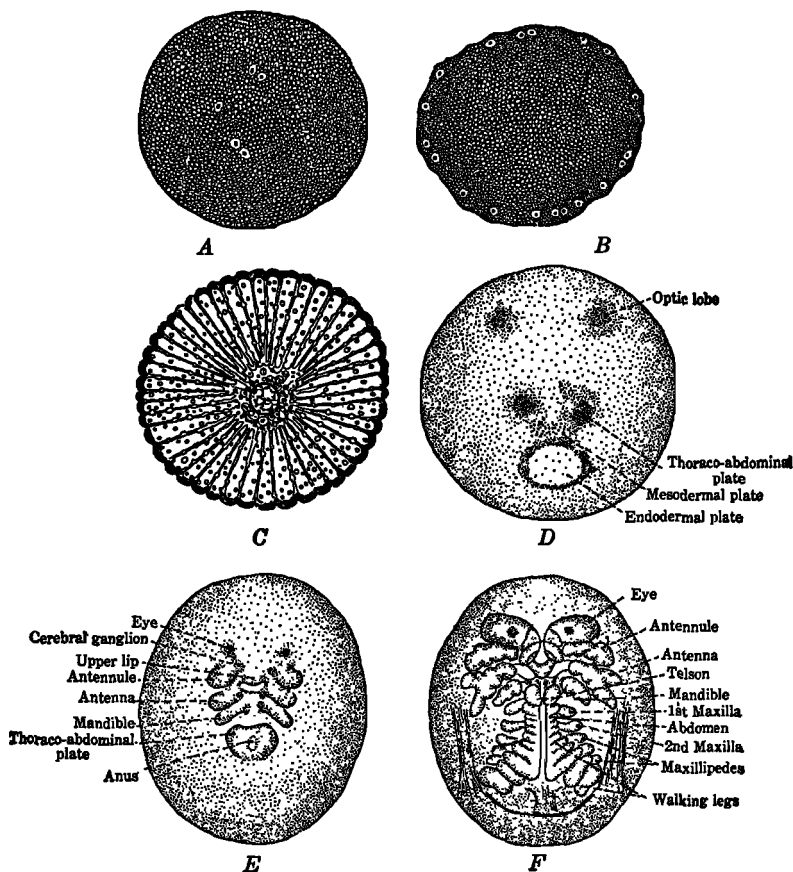


FIG. 271. — Stages in the embryology of the crayfish. A, egg with a few cleavage nuclei. B, nuclei arranged near the surface. C, egg divided into yolk pyramids. D, embryo beginning to form. E, embryo in *Nauplius* stage. F, older embryo. (After Reichenbach.)

is not hollow but has a *blastocel* filled with yolk globules, and a single layer of cells at the periphery which constitute the *blastoderm*. On one side of the egg the blastoderm cells increase in number and become columnar thus forming a *ventral plate*. Five

thickenings of the ventral plate are recognizable (*D*); these are two *cephalic lobes* from which the eyes and cerebral ganglia will develop, two *thoracico-abdominal rudiments*, and one *endodermal disk* at the anterior end of which mesoderm cells are destined to arise. An invagination at the anterior end of the endodermal disk indicates the beginning of *gastrulation*.

Further changes in the ventral plate result in what is known as the *Nauplius* stage as illustrated in figure 271, *E*. At this time the following rudiments are recognizable: two cephalic lobes with cerebral rudiments in the center; three pairs of outgrowths which develop into the first and second antennæ and the mandibles; the upper lip or labium; the crescent-shaped mouth; and the anus in the center of the thoracico-abdominal disk.

As development continues the thoracico-abdominal disk grows out into a long forked process which bends underneath the egg toward the anterior end as shown in figure 271, *F*. The following pairs of rudiments may now be seen: optic lobes, optic ganglia, cerebral ganglia, antennal ganglia, first antennæ, second antennæ, mandibles, first and second maxillæ, first, second, and third maxillipeds, and first to fifth walking legs. The abdominal segments with the telson at the end are less distinct; the labium is a triangular outgrowth; and the fold that becomes the carapace is now visible.

The length of time required for the various stages in development was found by Andrews to be as follows: "Cleavage took up the first week, the beginning of an embryo the second week, to progress as far as the *Nauplius* the third week and more, to enlarge the embryo over one half of the egg a fourth week and more, and to perfect the embryo for hatching a fifth and sixth week or more. The whole egg development required from five to eight weeks in different sets of eggs under different temperature."

*Hatching*. — In hatching, the egg capsule splits and the larva emerges head foremost. The helpless young crayfish would drop away from the mother at once but for a thread extending from its telson to the inner surface of the egg capsule.

Soon the larva possesses strength enough to grasp the egg string with its claws. The telson thread then breaks. After about forty-eight hours the larva passes into a *second stage*. This is inaugurated by the shedding of the first larval cuticular covering, a process known as *molting* or *ecdysis*. This casting off of the

covering of the body is not peculiar to the young, but occurs in adult crayfishes as well as in young and adults of many other animals. In the larval crayfish the cuticle of the first stage becomes loosened and drops off. In the meantime the hypodermal cells have secreted a new covering. Ecdysis is necessary before growth can proceed, since the chitin of which the exoskeleton is composed does not allow expansion. In adults it is also a means of getting rid of an old worn-out coat and acquiring a new one.

In the *second larval stage* the young crayfish is again supported immediately after casting off its covering by a thread extending from the new to the old telson. When the larva becomes strong enough, it grasps the old larval skin or swimmerets, and the telson thread drops off. The duration of the second larval stage is about six days.

No telson thread is present after the molt which ushers in the *third larval stage*, but the young is able at once to cling to the old cuticle. In about a week the third larvæ become entirely independent of the mother, although they at first always return to her when separated. From this time on the larvæ shift for themselves, growing rapidly, and molting at least four more times during the first summer. The first winter no growth nor molts occur. There are four or five molts the second summer, three or four in the third summer, and perhaps one or two in the fourth summer. The life of a single individual extends over a period of about three or more years.

**Regeneration.**—The crayfish and many other crustaceans have the power of regenerating lost parts, but to a much more limited extent than such animals as *Hydra* and the earthworm. Experiments have been performed upon almost every one of the appendages as well as the eye. The second and third maxillipeds, the walking legs, the swimmerets, and the eye have all been injured or extirpated at various times and subsequently renewed the lost parts. Many species of crayfish of various ages have been used for these experiments. The growth of regenerated tissue is more frequent and rapid in young specimens than in adults.

The new structure is not always like that of the one removed. For example, when the annulus containing the sperm receptacle of an adult is extirpated, another is regenerated, but, although this is as large as that of the adult, it is comparable in complexity to that of an early larval stage. A more remarkable phenomenon

is the regeneration of an apparently functional (tactile) antenna-like organ in place of a degenerate eye which was removed from the blind crayfish, *Cambarus pellucidus testii*. In this case a non-functional organ was replaced by a functional one of a different character. The regeneration of a new part which differs from the part removed is termed *heteromorphosis*.

**Autotomy.** — Perhaps the most interesting morphological structure connected with the regenerative process in *Cambarus* is the definite breaking point near the bases of the walking legs. If the chelæ are injured, they are broken off by the crayfish at the breaking point. The other walking legs, if injured, may be thrown off at the free joint between the second and third segments. A new leg, as large as the one lost, develops from the end of the stump remaining. This breaking off of the legs at a definite point is known as *autotomy*, a phenomenon that also occurs in a number of other animals. The breaking point in decapod crustaceans is in the base of the ischium. The leg is flexed by the autotomizer muscle until the ischium comes in contact with the coxa. Continued pull of the autotomizer muscle separates the leg at the breaking point. The muscles are not damaged and the valve and diaphragm prevent hæmorrhage. Autotomy results when the leg is stimulated by some harmful agent or may be brought about in certain instances by injury to a ventral ganglion or by a strong general stimulus. Immediately after the leg has been thrown off, a membrane of ectoderm cells covers the canal through which the nerve and blood passed; five days later regeneration begins by an outward growth of the ectoderm cells which lined the exoskeleton. An interesting point in this new growth is that the muscles of the regenerated part are probably produced by ectoderm cells, whereas in the embryonic development of the crayfish the muscles are supposed to arise from the endoderm.

The power of autotomy is of advantage to the crayfish, since the wound closes more quickly if the leg is lost at the breaking point. No one has yet offered an adequate theory to account for autotomy. It is probably "a process that the animal has acquired in connection with the condition under which it lives, or in other words, an adaptive response of the organism to its condition of life."

As in the earthworm, the *rate of regeneration* depends upon the amount of tissue removed. If one chela is amputated, a new chela

regenerates less rapidly than if both chelæ and some of the other walking legs are removed.

**Behavior.** — When at rest, the crayfish usually faces the entrance to its place of concealment, and extends its antennæ. It is thus in a position to learn the nature of any approaching object without being detected. Activity at this time is reduced to the movements of a few of the appendages and the gills; the scaphognathites of the second maxillæ move back and forth baling water out of the forward end of the gill chambers; the swimmerets are in constant motion creating a current of water; the maxillipeds are likewise kept moving; and the antennæ and eye stalks bend from place to place.

Crayfishes are more active at nightfall and at daybreak than during the remainder of the day. At these times they venture out of their hiding places in search of food, their movements being apparently all utilitarian and not for spontaneous play or exercise.

**Locomotion.** — Locomotion is effected in two ways, walking and swimming. Crayfishes are able to walk in any direction, forward usually, but also sidewise, obliquely, or backward. In walking, the fourth pair of legs are most effective and bear nearly all of the weight of the animal; the fifth pair serve as props, and to push the body forward; the second and third pairs are less efficient for walking, since they are modified to serve as prehensile organs, and as toilet implements. Swimming is not resorted to under ordinary conditions, but only when the animal is frightened or shocked. In such a case the crayfish extends the abdomen, spreads out the uropods and telson, and, by sudden contractions of the bundles of flexor abdominal muscles, bends the abdomen and darts backwards. The swimming reaction apparently is not voluntary, but is almost entirely reflex.

**Equilibration.** — The crayfish either at rest or in motion is in a state of unstable equilibrium, and must maintain its body in the normal position by its own efforts. The force of gravity tends to turn the body over. From a large number of experiments it has been proven that the statocysts are the organs of equilibration. The structure of these organs is described on page 385. The contact of the statoliths with the statocyst hairs furnishes the stimulus which causes the animal to maintain an upright position.

When placed on its back, the crayfish has some difficulty in righting itself. Two methods of regaining its normal position are employed. The usual method is that of raising itself on one side and allowing the body to tip over by the force of gravity. The second method is that of contracting the flexor abdominal muscles which causes a quick backward flop, bringing the body right side up. In general, the animals "right themselves, when placed on their backs, by the easiest method; and this is found to depend usually upon the relative weight of the two sides of the body. When placed upon a surface which is not level, they take advantage, after a few experiences, of the inclination by turning toward the lower side."

*Senses and their location.* — The sense of *touch* in crayfishes is perhaps the most valuable, since it aids them in finding food, avoiding obstacles, and in many other ways. It is located in specialized hairs on various parts of the body. *Vision* in crayfishes is probably of minor importance, since the compound eyes are almost useless in recognizing form, and are of real value only in detecting moving objects. No reactions to *sound* have ever been observed in crayfishes, and apparently they do not hear. "The reactions formerly attributed to audition are probably due to tactile reflexes." In aquatic animals it is so difficult to distinguish between reactions of *taste* and *smell* that these senses are both included in the term *chemical sense*. The end organs of this sense are distributed all over the body.

*Reactions to stimuli.* — *Contact.* — The crayfish "is sensitive to touch over the whole surface of the body, but especially on the chelæ and chelipeds, the mouth parts, the ventral surface of the abdomen, and the edge of the telson." The antennæ are usually considered the special organs of touch, but experiments seem to prove that they are not so sensitive as other parts of the body. The tactile hairs are plumed, and supplied by a single nerve. *Positive* reactions to contact are exhibited by crayfishes to a marked degree, the animals seeking to place their bodies in contact with a solid object, if possible. The normal position of the crayfish when at rest under a stone is such as to bring its side or dorsal surface in contact with the walls of its hiding place. This, no doubt, is of distinct advantage, since it forces the animal into a place of safety.

*Light.* — Light of various intensities in the majority of cases causes the crayfish to retreat. Individuals prefer colored lights to

white, having a special liking for red. Negative reactions to light play an important rôle in the animal's life, since they influence it to seek a dark place where it is concealed from its enemies.

*Chemicals.* — The reactions of the crayfish to food are due in part to a chemical sense. Smooth hairs, with nerve bundles within them, are probably chemical, and, since "The animals react to chemical stimulation on any part of the body . . . we must assume that there are chemical sense organs all over the body." The anterior appendages, however, are the most sensitive, especially the outer ramus of the antennule. *Positive reactions* result from the application of food substances. For example, if meat juice is placed in the water near an animal, the antennæ move slightly and the mouth parts perform vigorous chewing movements. The meat causes "general restlessness and vague movements toward the source of the stimulation, but the animals seem to depend chiefly on touch for the accurate localization of food." Acids, salts, sugar, and other chemicals produce a sort of *negative reaction* indicated by scratching the carapace, rubbing the chelæ, or pulling at the part stimulated.

*Habit formation.* — It has been shown by certain simple experiments that crayfishes are able to learn habits and to modify them. They learn by experience, and modify their behavior slowly or quickly, depending upon their familiarity with the situation. The "chief factors in the formation of such habits are the chemical sense (probably both smell and taste), touch, sight, and the muscular sensations resulting from the direction of turning. The animals are able to learn a path when the possibility of following a scent is excluded."

## (2) OTHER CRUSTACEA

The CRUSTACEA are arthropods most of which live in the water and breathe by means of gills. The body is divided into head, thorax, and abdomen, or the head and thorax may be fused, forming a cephalothorax. The head usually consists of five segments fused together; it bears two pairs of antennæ (feelers), one pair of mandibles (jaws), and two pairs of maxillæ. The thorax bears a variable number of appendages, some of which are usually locomotory. The abdominal segments are generally narrow and more mobile than those of the head and thorax; they bear appendages which are often reduced in size.

The families of CRUSTACEA are usually arranged in a number of subclasses, divisions, orders, and suborders. The classification adopted here is largely that of Calman.

SUBCLASS I. BRANCHIOPODA.

Order 1. ANOSTRACA. Ex. *Eubbranchipus*.

Order 2. NOTOSTRACA. Ex. *Apus*.

Order 3. CONCHOSTRACA. Ex. *Estheria*.

Order 4. CLADOCERA. Ex. *Daphnia*.

SUBCLASS II. OSTRACODA.

Order 1. MYODOCOPA. Ex. *Sarsiella*.

Order 2. PODOCOPA. Ex. *Cypris*.

SUBCLASS III. COPEPODA.

Order 1. EUCOPEPODA. Ex. *Cyclops*.

Order 2. BRANCHIURA. Ex. *Argulus*.

SUBCLASS IV. CIRRIPIEDIA.

Order 1. THORACICA. Ex. *Lepas*.

Order 2. ACROTHORACICA. Ex. *Alcippe*.

Order 3. RHIZOCEPHALA. Ex. *Sacculina*.

SUBCLASS V. MALACOSTRACA.

Division 1. PHYLLOCARIDA.

Order 1. NEBALIACEA. Ex. *Nebalia*.

Division 2. SYNCARIDA.

Order 1. ANASPIDACEA. Ex. *Anaspides*.

Division 3. PERICARIDA.

Order 1. MYSIDACEA. Ex. *Mysis*.

Order 2. CUMACEA. Ex. *Diastylis*.

Order 3. ISOPODA. Ex. *Asellus*.

Order 4. AMPHIPODA. Ex. *Gammarus*.

Division 4. EUCARIDA.

Order 1. DECAPODA. Ex. *Cambarus*.

Division 5. HOPLOCARIDA.

Order 1. STOMATOPODA. Ex. *Squilla*.

Lack of space prevents a detailed description of all of the orders of the CRUSTACEA, hence some of those that contain the more common or interesting species have been selected for consideration.

SUBCLASS I. BRANCHIOPODA. — These are free-swimming crustaceans with flattened, leaf-like thoracic appendages that are respiratory in function. There is usually a carapace.

Order 1. ANOSTRACA. — Body elongate; eyes stalked; thoracic segments many, similar; no carapace. Ex. *Eubbranchipus vernalis*.



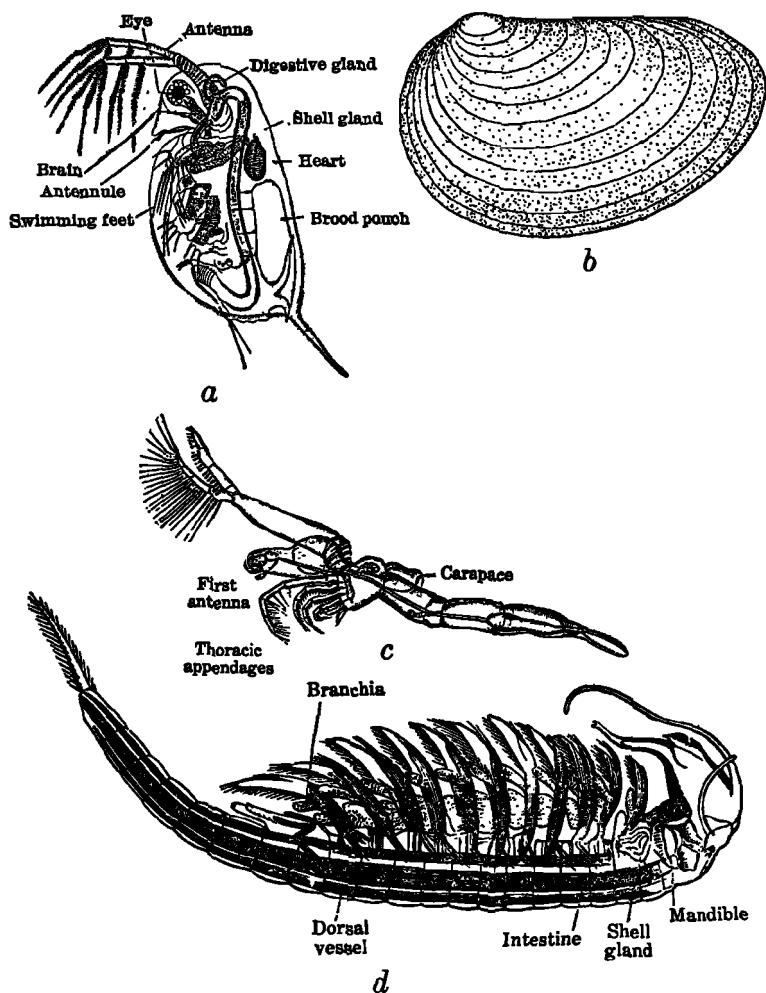


FIG. 272. — BRANCHIPODA. a, CLADOCERA. *Daphnia*. b, CONCHOSTRACA. *Estheria*. c, CLADOCERA. *Leptodora*. d, ANOSTRACA. *Branchipus*. (a, after Claus; b, after Sars; c, after Smith; d, after Sedgwick.)

(Fig. 272, *d*): fairy shrimp; color pinkish; fresh-water pools, especially in spring; eastern North America.

**Order 2. NOTOSTRACA.** — Body elongate; eyes sessile; thoracic segments many; carapace broad, shield-shaped. Ex. *Apus lucasani*: about 4 cm. long; in fresh water; western United States.

**Order 3. CONCHOSTRACA.** — Body enclosed in carapace in the form of a bivalve shell; eyes sessile; antennæ large, biramous. Ex. *Estheria morsei* (Fig. 272, *b*): shell about 12 mm. long; central and western United States.

**Order 4. CLADOCERA.** — Bivalve carapace usually covers the body but not the head; eyes sessile; antennæ large, biramous; four to six thoracic segments. Ex. *Daphnia pulex* (Fig. 272, *a*): water flea; color reddish; sharp caudal spine; ventral beak large; America. *Simcephalus vetulus*: no caudal spine; eastern United States. *Leptodora hyalina* (Fig. 272, *c*): shell small; abdomen terminated by two claws; antennæ large in male.

**SUBCLASS II. OSTRACODA.** — Free-swimming crustaceans with a bivalve carapace; compound eyes present or absent; two or less thoracic, non-phyllopod appendages; mandibular palp, usually biramous.

**Order 1. MYODOCOPA.** — Marine; second antennæ biramous, one branch large, the other small; deep notch in anterior margin of shell. Ex. *Sarsiella zostericola*: three eyes present; notch in shell (antennal sinus) absent in female; eastern United States.

**Order 2. PODOCOPA** (Fig. 273). — Mostly in fresh water; second antennæ uniramous; no notch in anterior margin of shell. Ex. *Cypris virens*: in fresh water; shell covered with short hairs; one median eye; second antennæ with five natatory bristles; partheno-

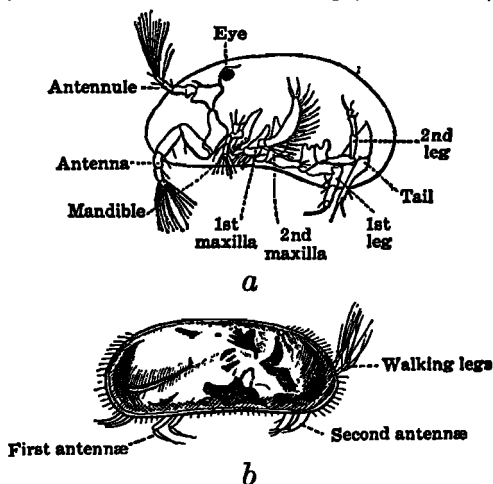


FIG. 273. — OSTRACODA. *a*, *Cypris*. *b*, *Candona*. (*a*, after Zenker, *b*, after Baird.)

genetic; no males known; cosmopolitan. *Loxoconcha impressa*: marine; Vineyard Sound.

**SUBCLASS III. COPEPODA.** — Free-swimming or parasitic; compound eyes and carapace absent; typically with six pairs of thoracic appendages.

**Order 1. EUCOPEPODA.** — Body elongate; female carries egg sacs; mouth parts chewing or sucking. Ex. *Calanus finmarchicus*: marine; antennæ very long; one egg sac; yellow or red; pelagic; important as fish food; New England coast. *Diaptomas sanguineus*: in fresh water; bright red; about 2 mm. long; in pools in spring; central and eastern United States. *Cyclops viridis* (Fig. 274, a): water flea; abdomen narrower than thorax; two egg sacs; usually greenish; small ponds; United States and Europe. *Ergasilus versicolor*: parasitic; dis-

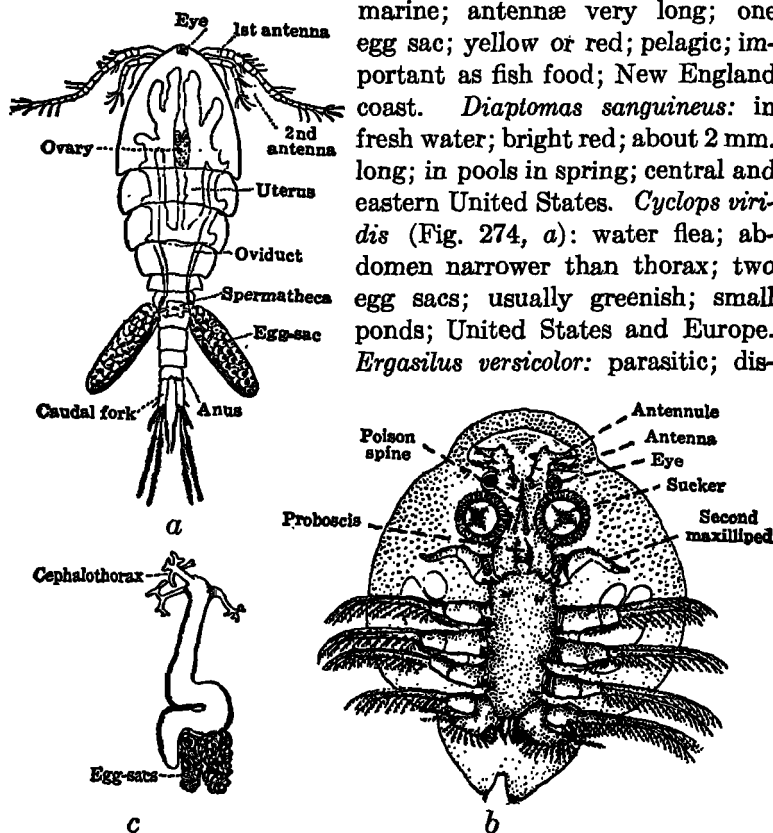


FIG. 274. — COPEPODA. a, *Cyclops*: dorsal view of female. b, *Argulus*: ventral view of female. c, *Lernæa*, parasite of a fish (haddock). (a, after Hartog; b, after Wilson; c, after Scott.)

tinctly segmented; on gills of bullhead and catfish. *Lernæa branchialis* (Fig. 274, c): parasitic; body of fertilized female, worm-like, twisted; two convoluted egg sacs; on gills of codfish, etc.

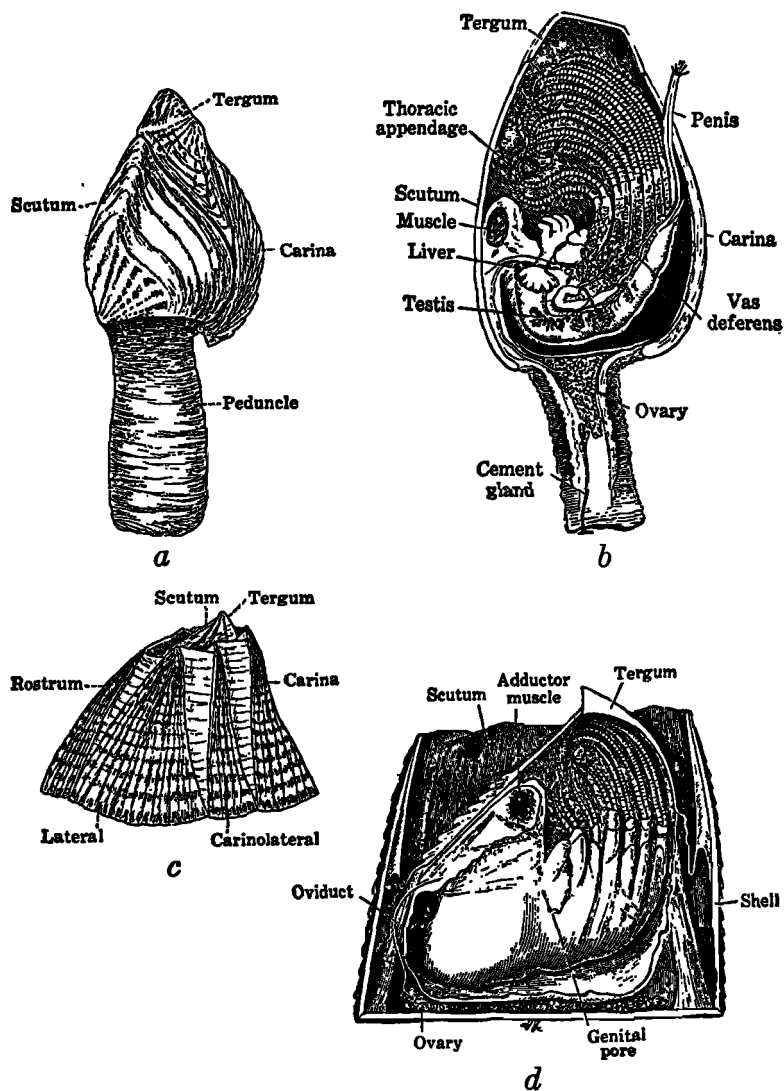


FIG. 275. — CIRRIPIEDIA. THORACICA. a, *Lepas*, external view. b, *Lepas*, internal view. c, *Balanus*, external view. d, *Balanus*, internal view. (a, b, after Darwin; c, d, after Claus.)

**Order 2. BRANCHIURA.** — Parasitic; no egg sacs; body flattened; five pairs of thoracic appendages. Ex. *Argulus laticauda* (Fig. 274, b): fish louse; suckers and a sting present; about 6 mm. long; on eel, flounder, etc.

**SUBCLASS IV. CIRRIPIEDIA.** — Sessile as adults; no compound eyes in adult; carapace enclosing body; mostly hermaphroditic.

**Order 1. THORACICA.** — Barnacles; marine; body surrounded by calcareous shell; six pairs of biramous thoracic legs. Ex. *Lepas*

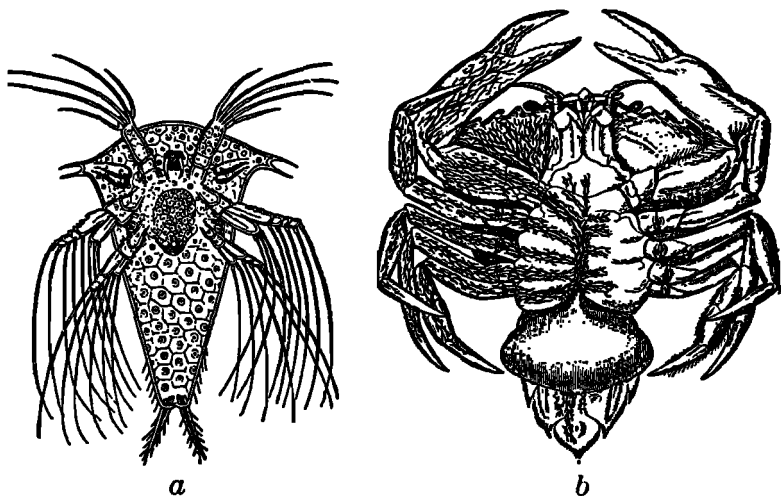


FIG. 276. — CIRRIPIEDIA. RHIZOCEPHALA. *Sacculina*. a, Nauplius larva. b, Adult attached like a sac to the undersurface of the abdomen of a crab and sending "roots" throughout the crab's body for extracting nourishment. (After Leuckart.)

*fascicularis* (Fig. 275 a, b): goose barnacle; body attached by short stalk; shell of five thin plates; cosmopolitan. *Balanus balanoides* (Fig. 275, c, d): rock barnacle; shell thick, closed by two hinged plates; stalk absent; North Atlantic coast.

**Order 2. ACROTHORACICA.** — Parasitic; no calcareous shell; body covered by large mantle. Ex. *Alcippe lampas*: males, small, legless, and attached to females; bores into *Natica* shells containing hermit crabs: Woods Hole, Mass.

**Order 3. RHIZOCEPHALA.** — Parasitic; no appendages, alimentary canal nor segmentation in adult; attached by stalk with roots penetrating tissue of host. Ex. *Sacculina carcini* (Fig. 276):

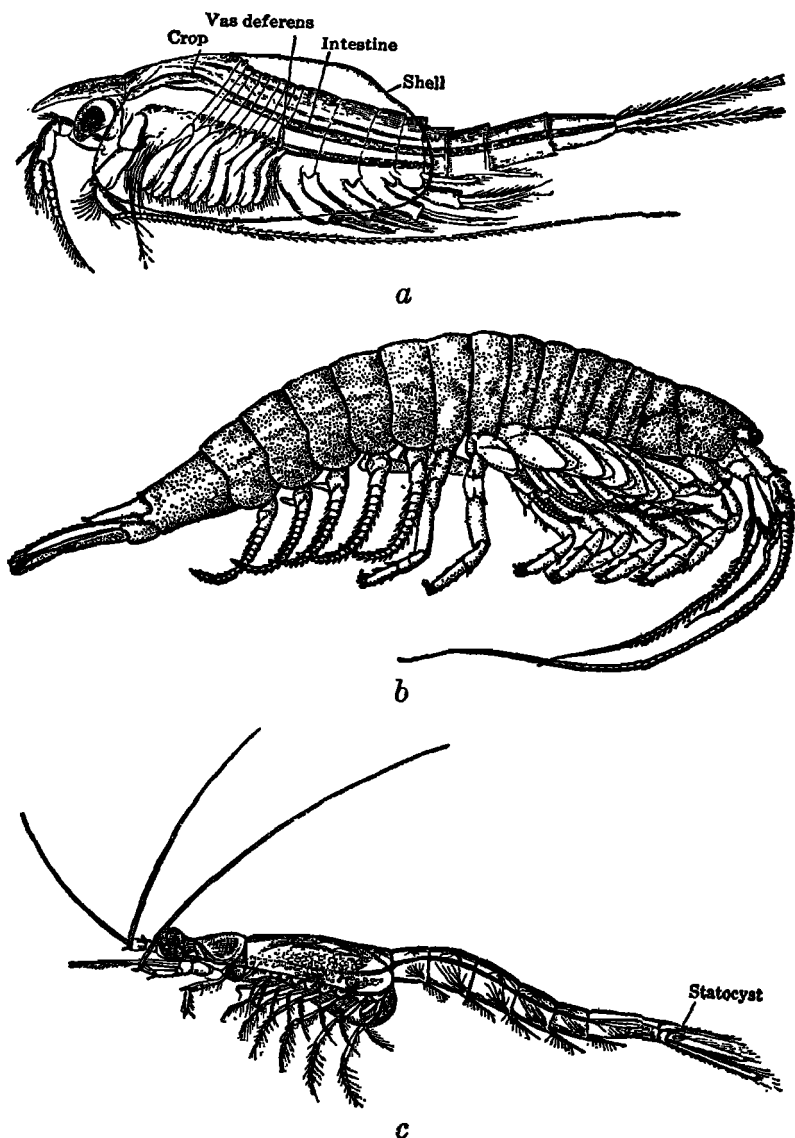


FIG. 277. — MALACOSTRACA. a, NEBALIACEA; *Nebalia geoffroyi*. b, ANASPIDACEA; *Anaspides tasmaniae*. c, MYSIDACEA; *Mysis oculata*. (a, after Claus; b, after Woodward; c, after Sars.)

parasitic on decapod crustaceans degenerating into a sac lying on the ventral surface between the thorax and abdomen.

**SUBCLASS V. MALACOSTRACA.** — Lobsters, crayfish, crabs, etc.: mostly large crustaceans; usually five segments in the head, eight in the thorax, and six in the abdomen; gastric mill in the stomach.

**Order 1. NEBALIACEA** (Fig. 277, *a*). — Primitive marine MALACOSTRACA with seven abdominal segments; stalked eyes; thorax

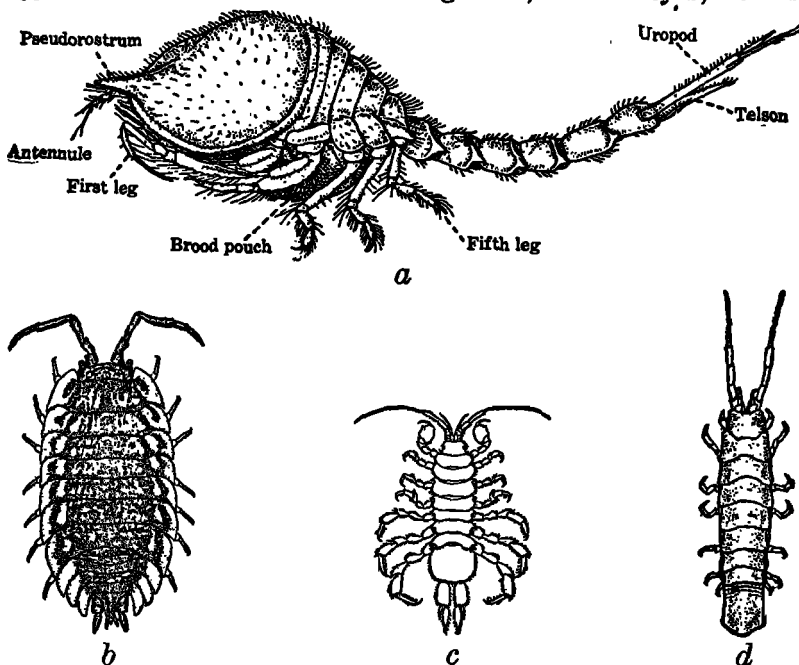


FIG. 278. — MALACOSTRACA. *a*, CUMACEA: *Diastylis goodsiri*. *b*, ISOPODA; *Oniscus asellus*. *c*, ISOPODA; *Asellus communis*. *d*, ISOPODA; *Idothea rectilinea*. (*a*, after Sars; *b*, after Smith; *c*, after Paulmier; *d*, after Johnson and Snook.)

with eight pairs of leaf-like gills. Ex. *Nebalia bipes*: body slender, compressed; eggs carried by setæ on the thoracic appendages of female.

**Order 2. ANASPIDACEA.** — Fresh water; no carapace; a tail fan. Ex. *Anaspides tasmanica* (Fig. 277, *b*): from ponds in Tasmania.

**Order 3. MYSIDACEA** (Fig. 277, *c*). — Carapace covers almost entire thorax; eyes stalked; thoracic appendages all biramous. Ex. *Mysis stenolepis*: body elongate, cylindrical; abdomen bends between first and second segments; Atlantic coast of North America.

**Order 4. CUMACEA** (Fig. 278, *a*). — Carapace does not cover entire thorax; eyes sessile; no tail fan. Ex. *Diastylis quadrispinosus*: a spine on each side of carapace; New Jersey northward.

**Order 5. ISOPODA.** — Marine, fresh water, terrestrial, or parasitic; eyes sessile; body flattened dorso-ventrally. Ex. *Asellus communis* (Fig. 278, *c*): common among vegetation in fresh water; eastern United States. *Oniscus asellus* (Fig. 278, *b*): sow bug; terrestrial, under stones, logs, bark, etc.; central and eastern United States, Europe. *Livoneca ovalis*: parasitic on gills and in mouth of bluefish; Cape Cod southward. *Idothea baltica* (Fig. 278, *d*); marine; cosmopolitan.

**Order 6. AMPHIPODA.** — Mostly marine; usually laterally compressed; eyes sessile; no carapace; no tail fan. Ex. *Talorchestia longicornis*: beach flea; body large; two large eyes; on sand beaches; Cape Cod to New Jersey. *Gammarus fasciatus* (Fig. 279, *a*): in fresh-water ponds and streams; eastern United States. *Caprella geometrica* (Fig. 279, *b*): body elongate, slender; on seaweeds and hydroids; Cape Cod to Virginia.

**Order 7. DECAPODA.** — Lobsters, crayfish, shrimps, crabs. This order contains six or more thousand species of comparatively large and familiar crustaceans. The carapace covers the entire thorax; three pairs of maxillipeds; five pairs of thoracic walking legs, the first pair usually larger and with pinching claws (chelæ); mostly marine. Ex. *Homarus americanus*: lobster; marine. *Cambarus bartoni*: crayfish; eastern states. *Crago vulgaris*: edible shrimp; South Carolina northward, Pacific coast, Europe. *Palæmonetes vulgaris* (Fig. 280, *a*): prawn; eastern coast. *Emerita talpoida*: sand bug; Cape Cod to Florida, Pacific coast. *Pagurus longicarpus* (Fig. 280, *b, c*): small hermit crab; Maine to South Carolina. *Libinia emarginata*: spider crab; Atlantic coast. *Cancer irroratus*: rock crab; edible; South Carolina northward. *Calli-*

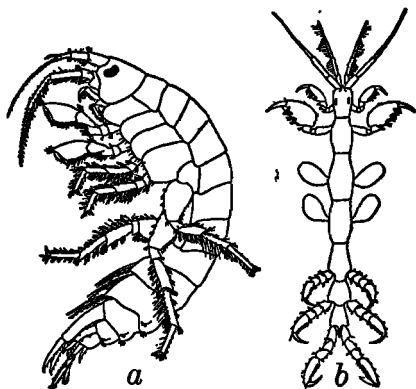


FIG. 279. — MALACOSTRACA. AMPHIPODA. *a*, *Gammarus fasciatus*. *b*, *Caprella geometrica*. (From Paulmier.)



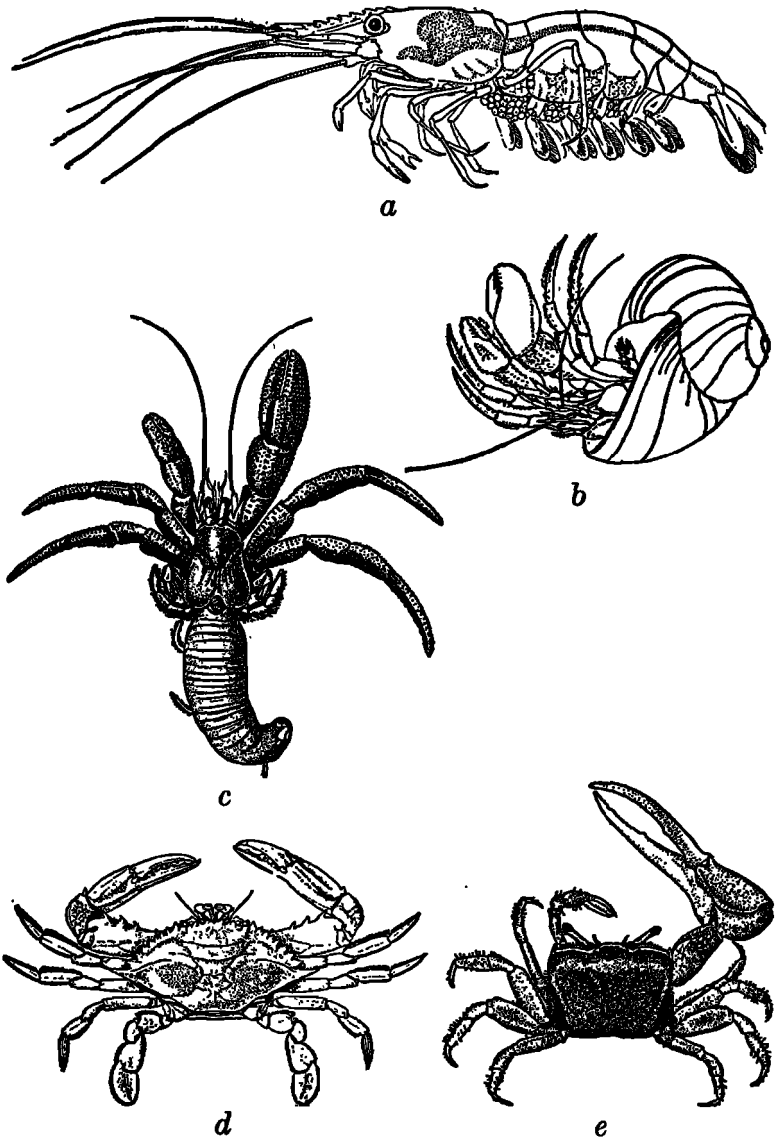


FIG. 280. — MALACOSTRACA. DECAPODA. *a*, *Palæmonetes vulgaris*, the prawn. *b*, *Pagurus*, the hermit crab, in snail shell. *c*, *Pagurus*, removed from snail shell. *d*, *Callinectes sapidus*, the edible or blue crab. *e*, *Uca crenulata*, the fiddler crab. (*a*, from Davenport; *b*, after Emerton; *c*, after Cuvier; *d*, after Rathbun; *e*, after Johnson and Snook.)

*nectes sapidus* (Fig. 280, d): blue or edible crab; eastern coast. *Uca pugnax*: fiddler crab (Fig. 280, e); eastern coast.

**Order 8. STOMATOPODA** (Fig. 281). — Marine; body elongate with broad abdomen; carapace covering three of seven thoracic segments; stalked eyes; gills on first five pairs of abdominal appendages; second pair of maxillipeds very large and subchelate. Ex. *Squilla empusa*: body up to 25 cm. long; in burrows in mud near shore; edible; eastern coast.

**CLASS TRILOBITA.** — The TRILOBITA are usually included in the phylum ARTHROPODA as a class, but are all extinct. They were

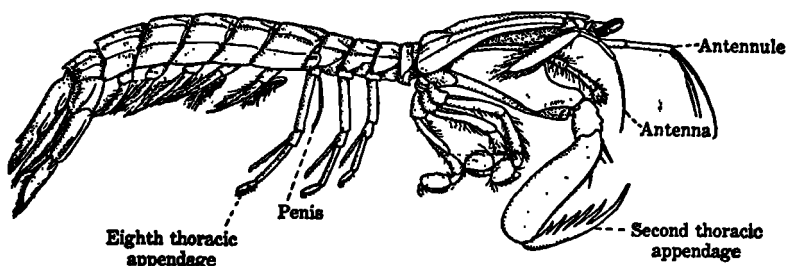


FIG. 281. — MALACOSTRACA. STOMATOPODA. *Squilla mantis*, male. (After Calman.)

marine animals, especially abundant in the Cambrian and Silurian. One pair of antennæ was present. Each segment posterior to the antennary somite bore a pair of biramous appendages each with a gnathopod. Trilobites are associated in the strata of the earth's crust with the remains of crinoids, brachiopods, and cephalopods. The best-known species, *Triarthrus becki*, occurs in the Utica shale (Lower Silurian) of New York state.

## 2. CLASS II. ONYCHOPHORA

The ten genera and seventy odd species belonging to this class are all usually referred to as *Peripatus* (Fig. 282). They are espe-

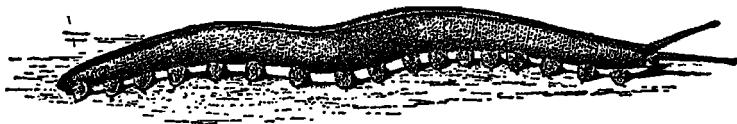


FIG. 282. — ONYCHOPHORA. *Peripatus capensis*. (After Sedgwick.)

cially interesting because they evidently separated from the main arthropodan stock at an early period and obviously exhibit both

arthropod and annelid characteristics as well as peculiarities of their own. Unfortunately they are very rare and hence not available for laboratory study. The genera thus far described and their geographical distribution are as follows:

(1) *Peripatus*, tropical America; (2) *Oroperipatus*, Pacific watershed of tropical America; (3) *Metaperipatus*, Chile; (4) *Paraperipatus*, New Britain, New Guinea, and Ceram; (5) *Mesoperipatus*, French Congo; (6) *Peripatopsis*, Cape Colony and Natal; (7) *Opisthopatus*, Cape Colony and Natal; (8) *Peripatoides*, Australia, Tasmania, and New Zealand; (9) *Eoperipatus*, Sumatra and Malay Peninsula; (10) *Typhloperipatus*, Tibet.

The group furnishes an excellent example of discontinuous distribution. Even in the area where a species occurs, specimens are present only in a few of the many available habitats. This seems to indicate that the class had once a continuous distribution but has disappeared throughout most of its range and is on the road to extinction.

*Peripatus* lives in crevices of rock, under bark and stones, and in other dark moist places and is active only at night. As the animal moves slowly from place to place by means of its legs, the two extremely sensitive antennæ test the ground over which it is to travel, while the eyes, one at the base of each antenna, enable it to avoid the light. When irritated, *Peripatus* often ejects slime, sometimes to the distance of almost a foot, from a pair of glands which open on the oral papillæ. This slime sticks to everything but the body of the animal itself; it is used principally to capture flies, wood-lice, termites, and other small animals, and in addition is probably a weapon of defense. A pair of modified appendages serve as jaws and tear the food to pieces.

Most species of *Peripatus* are viviparous, and a single large female may produce thirty or forty young in a year. These young resemble the adults when born, differing chiefly in size and color.

Figure 283 shows the principal internal organs of a male specimen. The head (Fig. 284, *b*) bears three pairs of appendages, the antennæ, oral papillæ, and jaws, a pair of simple eyes, and a ventrally placed mouth. The fleshy legs (Fig. 284, *c*) number from seventeen pairs to over forty pairs in different species; each bears two claws. The anus is at the posterior end (Fig. 284, *a*); the genital pore is situated between the last pair of legs; and a nephridiopore lies at the base of each leg. The skin is covered with

*papillæ*, each bearing a *spine*; these papillæ are especially numerous on the antennæ, lips, and oral papillæ, and are probably *tactile*. The external rings of the body are more numerous than the internal segments.

The *digestive system* (Fig. 283) is very simple, consisting of a muscular *pharynx*, a short *œsophagus*, a long, saccular *stomach*, and a short *intestine*.

The pair of *salivary glands*, which open into the mouth cavity, are modified nephridia. The *heart* is the only blood vessel; it is a dorsal tube with paired ostia connecting it with the pericardial cavity in which it lies. The *body cavity* is a blood space, *i.e.* a hæmocœl. The breathing organs are air-tubes, called *trachææ*, which open by means of pores on various parts of the body. The excretory organs are *nephridia*, one at the base of each leg. The vesicular end of the nephridium is part of the cœlom. The nervous system consists of a *brain*, dorsally situated in the head, and a pair of *ventral nerve*

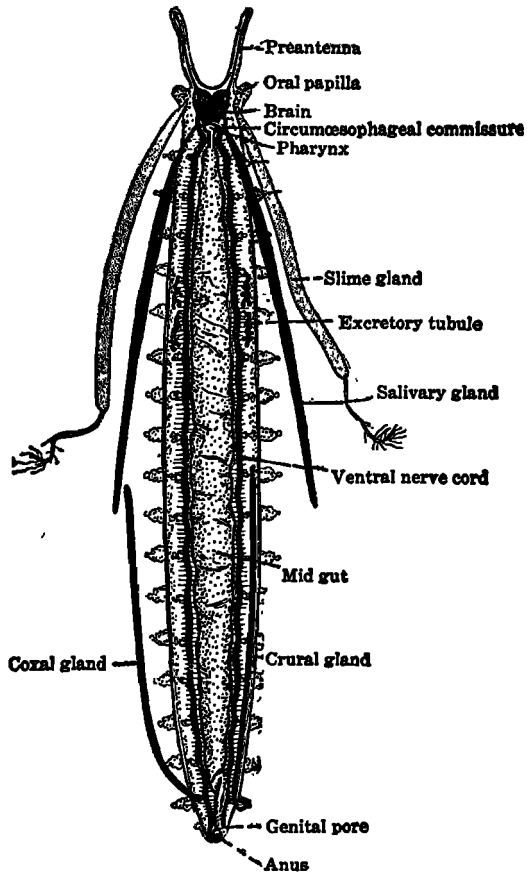


FIG. 283. — ONYCHOPHORA. *Peripatus capensis*. Dissection of male. (After Balfour, modified.)

*cords*, which are connected by many transverse nerves. The sexes are separate, and the cavities of the reproductive organs are cœlomic.

*Peripatus* is of special interest since its body exhibits certain

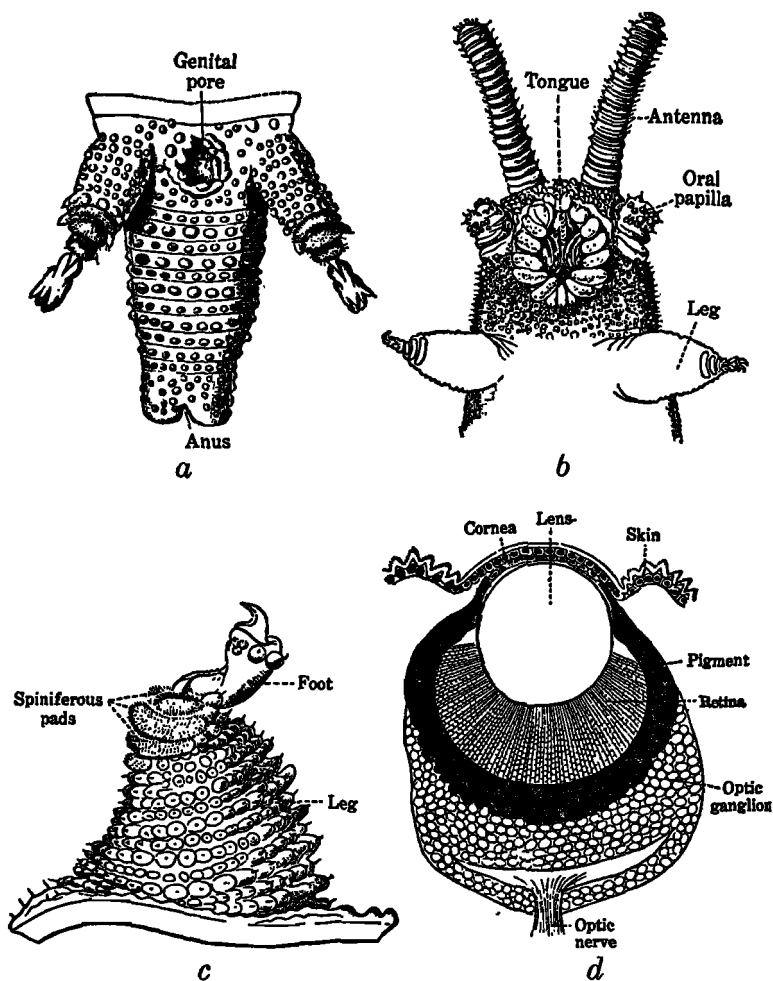


FIG. 284. — ONYCHOPHORA. Anatomy of *Peripatus*. a, Posterior end, ventral view. b, Anterior end, ventral view. c, Leg, front view. d, Eye, longitudinal section. (From Sedgwick; d, after Balfour.)

structures characteristic of annelids and other structures found only in arthropods. It is, however, undoubtedly an arthropod. The accompanying table presents briefly these characteristics and shows in what respects it differs from other arthropods:—

THE CHARACTERISTICS OF PERIPATUS ARRANGED SO AS TO SHOW THE SIMILARITY TO AND DIFFERENCES FROM ARTHROPODS AND ANNELIDS

ARTHROPOD CHARACTERISTICS	ANNELID CHARACTERISTICS	STRUCTURES PECULIAR TO PERIPATUS
Appendages modified as jaws	Paired segmentally arranged nephridia	Number and diffusion of tracheal apertures
A hæmocœlic body cavity	Cilia in reproductive organs	Single pair of jaws
No cœlom around alimentary canal	Chief systems of organs arranged as in annelids	Distribution of reproductive organs
Tracheæ present		Texture of skin
		Simplicity and similarity of segments behind the head

### 3. CLASS III. CHILOPODA

The CHILOPODA are called centipedes (Fig. 286). The body is flattened dorso-ventrally, and consists of from fifteen to one hundred seventy-three segments, each of which bears one pair of legs except the last two and the one just back of the head. The latter bears a pair of poison claws called maxillipeds, with which insects, worms, mollusks, and other small animals are killed for food. The antennæ are long consisting of at least twelve segments.

The internal anatomy of a common centipede is shown in figure 285. The alimentary canal is simple; into it open the excretory organs—two Malpighian tubules. The tracheæ are branched as in insects and open by a pair of stigmata in almost every segment. The reproductive organs are connected with several accessory glands. Eggs are usually laid. Those of *Lithobius* are laid singly and covered with earth.

The centipedes are swift-moving creatures. Many of them live under the bark of logs, or under stones. The genera *Lithobius*, *Geophilus*, and *Scutigera* are common. The poisonous centipedes of tropical countries belong to the genus *Scolopendra*. They may reach a foot in length, and their bite is painful and even dangerous to man. Fossil CHILOPODA have been found in amber of oligocene age. Four of the families in this class are as follows:

Family 1. GEOPHILIDÆ (Fig. 286, a). — Body long, with over 31 segments; eyes absent; antennæ with 14 segments; young leave egg with full number of segments and legs. Ex. *Geophilus rubens*:

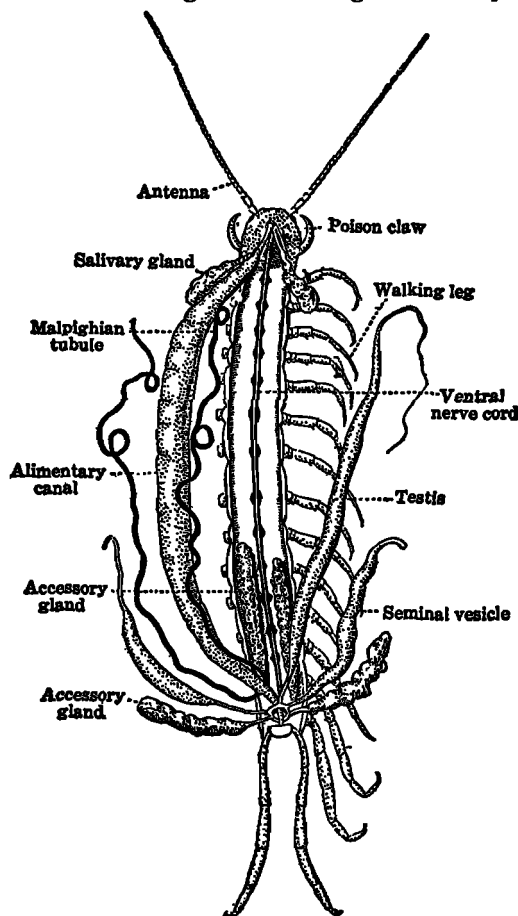


FIG. 285. — CHILOPODA. *Lithobius forficatus*, dissected to show the internal organs. (After Vogt and Jung, after Sedgwick.)

about 45 mm. long; 47 to 53 pairs of legs; eastern and central states.

Family 2. SCOLOPENDRIDÆ. — Body long, with 21 to 23 segments; eyes present or absent; antennæ with 17 to 31 segments; young leave egg with full number of segments and legs. Ex. *Scolopendra morsitans* (Fig. 286, b): 21 pairs of legs; eyes present;

cosmopolitan. *Scolopocryptops sexspinosa*: 23 pairs of legs; eyes absent; United States.

Family 3. LITHOBIDÆ. — Body with legs on 15 segments; maxillary palp with 3 segments; young leave egg with 7 pairs of

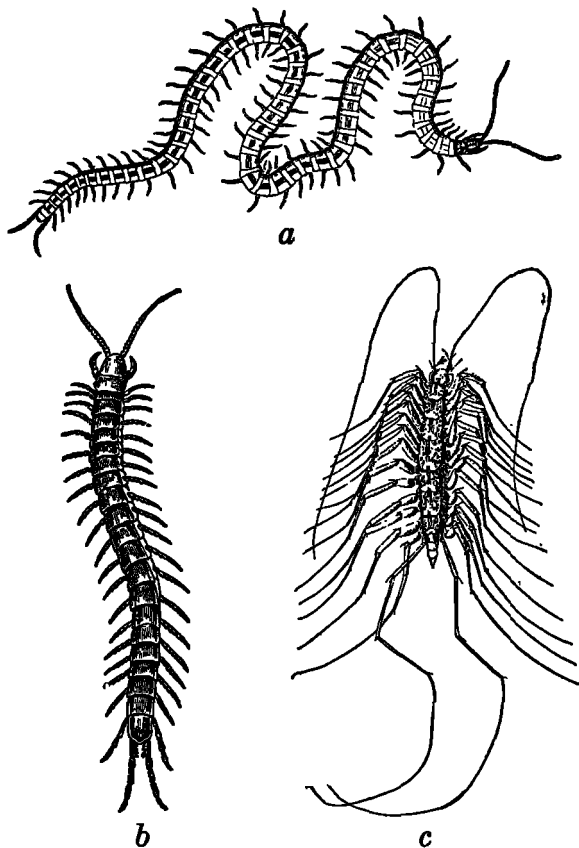


FIG. 286. — CHILOPODA. a, GEOPHILIDÆ; *Geophilus longicornis*. b, SCOLOPENDRIDÆ; *Scolopendra morsitans*. c, SCUTIGERIDÆ; *Scutigera forceps*. (b, from Cläus; c, from Herrick.)

legs. Ex. *Lithobius forficatus* (Fig. 285): body about 3 mm. long; antennæ with 33 to 43 segments; America, Europe.

Family 4. SCUTIGERIDÆ. — Body short, with about 15 segments; 15 pairs very long legs, last pair longest; antennæ very long. Ex. *Scutigera forceps* (Fig. 286, c): about 25 mm. long; last pair of legs about 50 mm. long; United States.



## 4. CLASS IV. DIPLOPODA

This class together with the CHILOPODA, PAUROPODA, and SYMPHYLA were formerly grouped together into a single class, the MYRIAPODA. The CHILOPODA, however, are more closely related to the insects than to the DIPLOPODA and the other two groups are not closely related hence it seems best to treat each as a distinct class.

The DIPLOPODA are called millipedes (Fig. 288). The body is subcylindrical, and consists of from about twenty-five to more

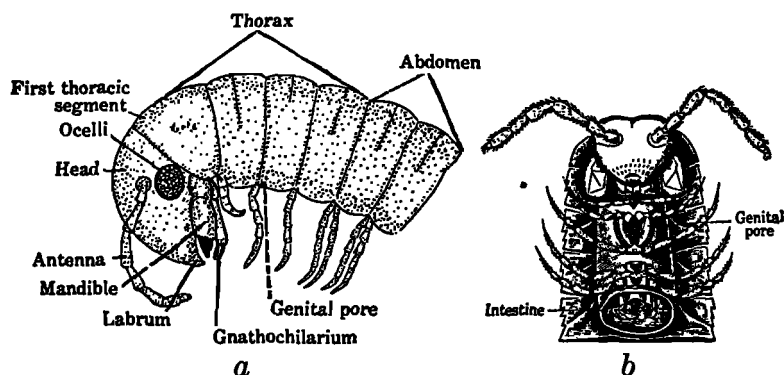


FIG. 287. — DIPLOPODA. a, *Julus terrestris*, side view of anterior end. b, *Polydesmus complanatus*, ventral view of anterior end. (a, after Borradale and Potts; b, after Latzel.)

than one hundred segments, according to the species. Almost every segment bears two pairs of appendages (Fig. 287), and has probably arisen by the fusion of two segments. One or both pairs of legs on the seventh segment of the male are modified as copulatory organs. The mouth parts are a pair of mandibles and a pair of maxillæ. One pair of short antennæ and either simple or aggregated eyes are usually present. There are olfactory hairs on the antennæ and a pair of scent glands in each segment, opening laterally. The breathing tubes (tracheæ) are usually unbranched; they arise in tufts from pouches which open just in front of the legs. The heart is a dorsal vessel with lateral ostia; it gives rise to arteries in the head. The two or four excretory organs are thread-like tubes (Malpighian tubules) which pour their excretions into the intestine.

The millipedes move very slowly in spite of their numerous

legs. Some of them are able to roll themselves into a spiral or ball. They live in dark, moist places and feed principally on decaying vegetable matter but sometimes on living plants and may thus be destructive. The sexes are separate, and the eggs are laid in damp earth. The young have few segments and only three pairs of legs when they hatch, and resemble apterous insects. Other segments are added just in front of the anal segment. Fossil millipedes have been discovered in geological formations as far back as the Devonian and Upper Silurian. Three of the families in this class are as follows:

Family 1. POLYXENIDÆ (Fig. 288, a). — Body small; integument soft; each segment with tuft of bristles on either side; maxil-

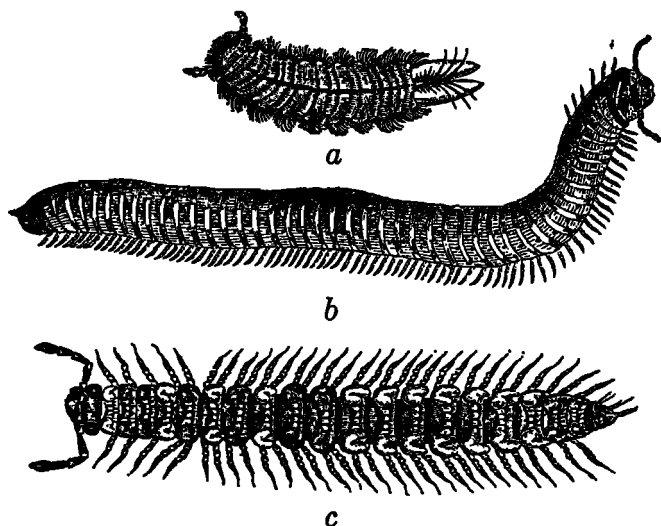


FIG. 288. — DIPLOPODA. a, POLYXENIDÆ; *Polyxenus lagurus*. b, JULIDÆ; *Julus nemorensis*. c, POLYDESMIDÆ; *Polydesmus collaris*. (From Koch.)

læ leg-like; no copulatory feet in male. Ex. *Polyxenus fasciculatus*: about 2.5 mm. long; 13 pairs of legs; Long Island and southern states.

Family 2. JULIDÆ (Fig. 288, b). — Integument hard; maxillæ form a plate; two pairs of copulatory feet on seventh segment of male. Ex. *Julus virgatus*: body with 30 to 35 segments; 50 to 60 pairs legs; no legs on third segment; body about 12 mm. long.

Family 3. POLYDESMIDÆ (Fig. 288, c). — Body with 19 to 22

segments; first pair of legs on seventh segment of male, copulatory. Ex. *Polydesmus serratus*: body about 37 mm. long; male with 30, female with 31 pairs of legs; eastern and central states.

## 5. CLASS V. INSECTA

### (1) DISSOSTEIRA CAROLINA — A GRASSHOPPER

The grasshopper is a favorable representative of the class INSECTA because it is less specialized than many of the other common insects and, therefore, exhibits insect characteristics in their more generalized condition.

**External features** (Plate VI; Fig. 289). — *Exoskeleton*. — As in the crayfish, the grasshopper is covered by an exoskeleton which

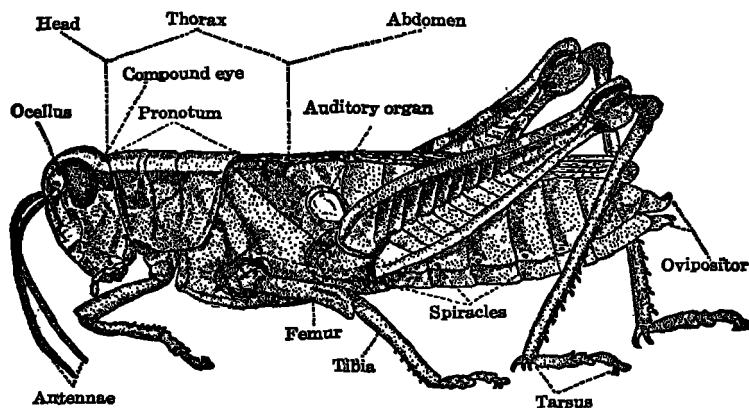


FIG. 289. — Diagram of a female grasshopper with wings removed on left side. (After Walden, from Wellhouse.)

protects the delicate systems of organs within. This exoskeleton is the *cuticula* which consists of chitin and is divided into a linear row of *segments*. The cuticula is mostly hard and rigid and some of the segments are firmly fastened together, but is softer between other segments thus allowing movements of the abdomen, wings, legs, antennæ, etc. These softer regions are known as *sutures*. The body wall consists of the cuticula beneath which is a layer of cells, the *hypodermis*, which secretes it and under this a *basement membrane*. Each segment is made up of separate pieces which are known as *sclerites*; usually some of the sclerites of a typical segment cannot be distinguished and the sutures are

therefore said to be obsolete. In the grasshopper the body is divided into three groups of segments that constitute the head, thorax, and abdomen.

*Head.* — Six segments are fused together to form the head. These are not visible in the adult but may be observed in the embryo and are indicated by the paired appendages of the adult. They are as follows: *preoral, antennal, intercalary, mandibular,*

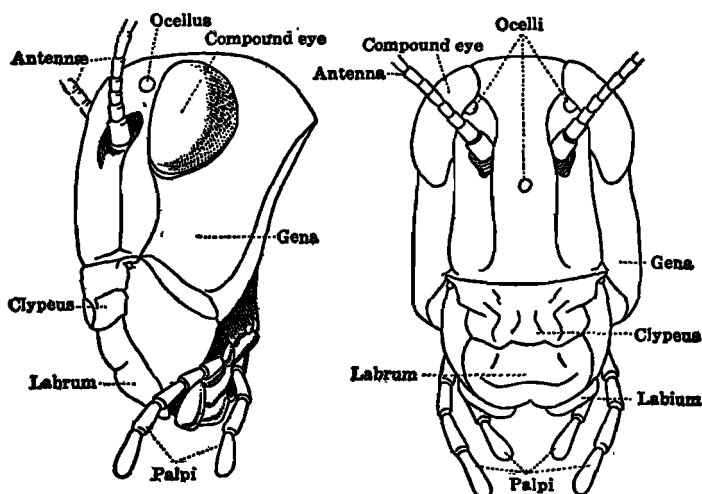


FIG. 290. — Head of a grasshopper in side and front views. (From Herms, after Folsom.)

*maxillary, and labial.* The exoskeleton of the head is known as the *epicranium*; the front of this is the *frons*, and the sides are the cheeks or *gena*. The rectangular sclerite beneath the front of the *epicranium* is the *clypeus*. On either side of the head is a *compound eye* and on top of the head and near the inner edge of each compound eye is a simple eye or *ocellus*. The mouth parts are attached to the ventral side of the *epicranium*.

*Mouth parts* (Fig. 291). — The grasshopper is a biting insect and its mouth parts are therefore *mandibulate*. There is a *labrum* or upper lip attached to the ventral edge of the *clypeus*. Beneath this is the membranous tongue-like organ, the *hypopharynx*. On either side is a single, hard jaw or *mandible* with a toothed surface fitted for grinding. Beneath the mandible are a pair of *maxillæ*; each of these consists of the following parts: a basal

*cardo*, central *stipes*, a long curved *lacinia*, a long, rounded *galea*, and a *maxillary palp* which arises from a *palpifer*. The *labium* or lower lip comprises a basal *submentum*, a central *mentum*, two movable flaps, the *ligulae*, and a *labial palp* on either side. The

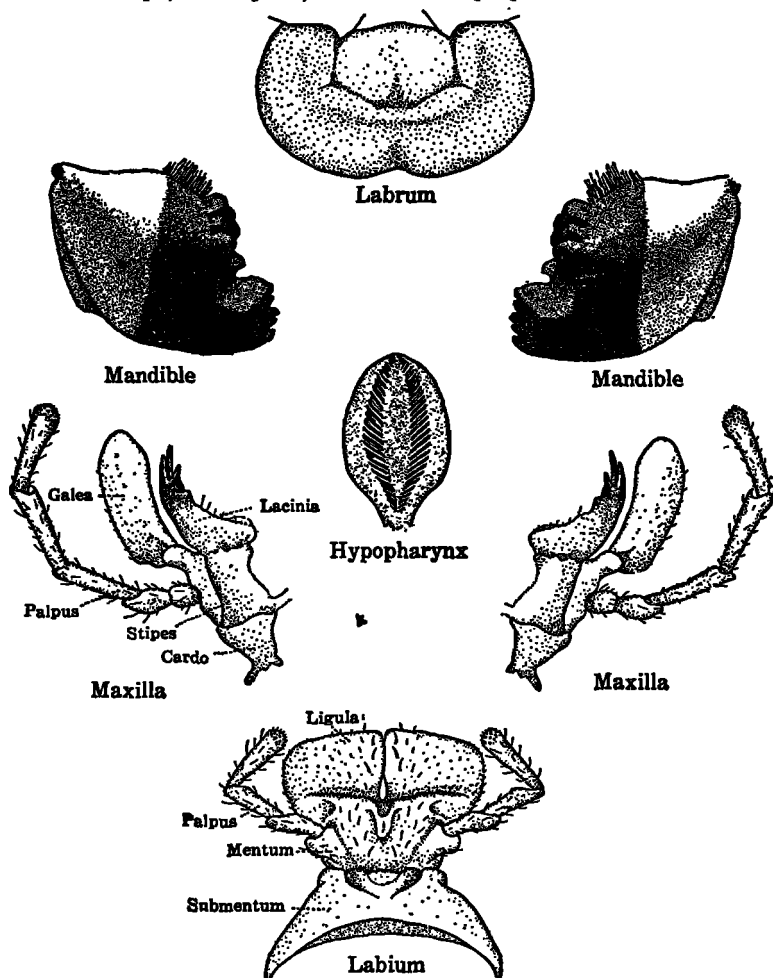


FIG. 291. — Mouth parts of a grasshopper. (From Hems.)

labium of the insects appears to have evolved from the lateral union of two appendages resembling the biramous limbs of a crustacean. The *maxillæ* have obviously also arisen from this type of appendage. The labrum and labium serve to hold food

between the mandibles and maxillæ which move laterally and grind it. The maxillary and labial palps are supplied with sense organs that no doubt serve to distinguish different kinds of food.

**Ocellus** (Fig. 292, b). — The simple eyes consist of a group of visual cells, the *retinulæ*, in the center of which is an optic rod, the *rhabdome*, and a transparent lens-like modification of the cuticula.

**Compound eye** (Fig. 292, a). — This is covered by a transparent part of the cuticula, the *cornea*, which is divided into a large number of hexagonal pieces, the *facets*. Each facet is the outer end of a unit known as an *ommatidium*. Such a structure gives mosaic

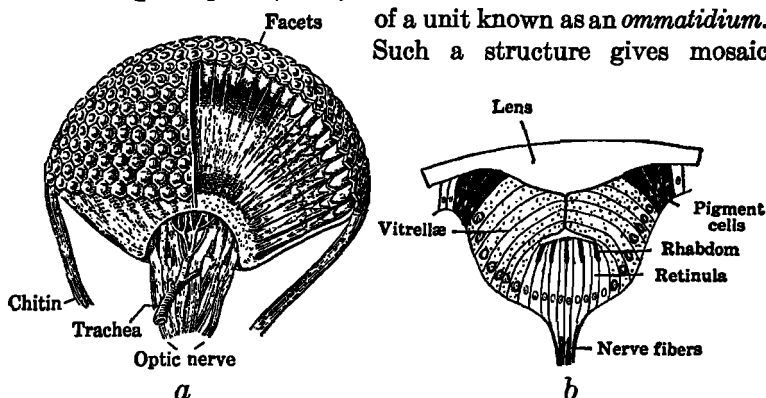


FIG. 292. — Diagrams of insect eyes. a, Compound eye. b, Simple eye or ocellus. (a, from Schmeil; b, from Borradaile and Potts, modified.)

vision as described in the crayfish (p. 385). Some insects, possibly the grasshopper, are able to distinguish colors.

**Antennæ.** — These are filiform in shape and consist of many joints. Sensory bristles, probably olfactory in nature, are present on them and this, combined with the ability of the insect to bend them about, makes them efficient sense organs.

**Thorax.** — This portion of the body is separated from the head and abdomen by flexible joints and consists of three segments which are an anterior prothorax, a middle mesothorax, and a posterior metathorax. Each segment bears a pair of legs and the mesothorax and metathorax each a pair of wings. On either side of the mesothorax and metathorax is a spiracle, an opening into the respiratory system.

**Prothorax.** — A typical segment includes ten sclerites. The dorsal *tergum* consists of four sclerites in a row, an anterior *præacu-*

tum followed by the *scutum*, *scutellum*, and *postscutellum*. The lateral *pleura* consist of three sclerites, the *episternum*, *epimeron*, and *parapteron*. The single ventral sclerite is the *sternum*. The *pronotum* of the prothorax is large and extends down on either

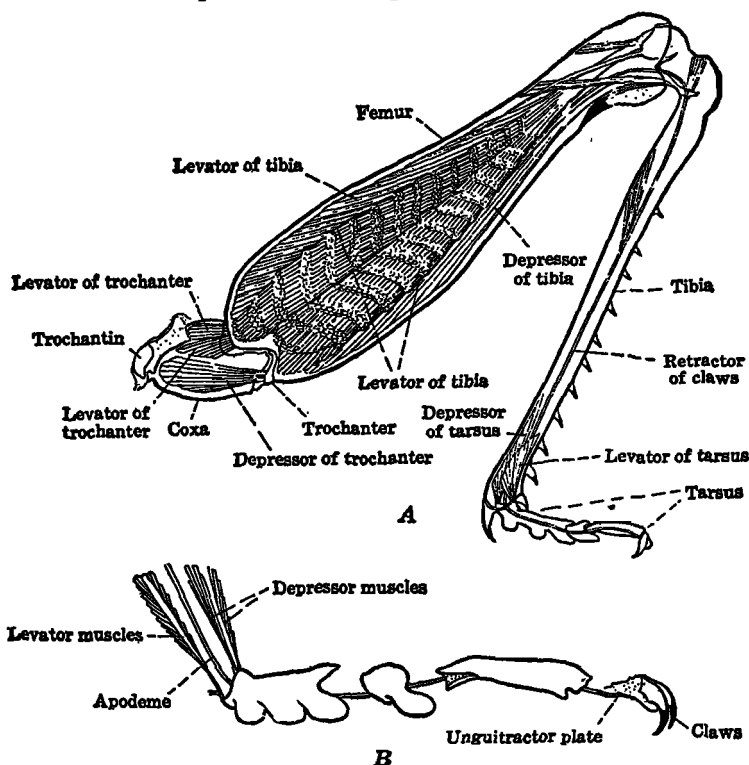


FIG. 293. — Carolina locust, *Dissosteira carolina*. A, Musculature of left, metathoracic leg. B, Tarsus of mesothoracic leg disjointed, showing levator and depressor muscles and tendon-like apodeme of retractor of claws attached to unguitractor plate and extending through tarsus. (After Snodgrass.)

side; its four sclerites are indicated by transverse grooves. The sternum bears a spine.

*Mesothorax*. — In this segment the tergum is small, but the sclerites of the pleurum are distinct.

*Metathorax*. — This resembles the mesothorax.

*Legs* (Fig. 293). — Each leg consists of a linear series of five segments as follows: the *coxa* articulates with the body; then come the small *trochanter* fused with the *femur*, the *tibia*, and the *tarsus*.

The femur of the metathoracic legs are enlarged to contain the muscles used in jumping. The tarsus (Fig. 293, *B*) of each leg consists of three visible segments; the one adjoining the tibia has

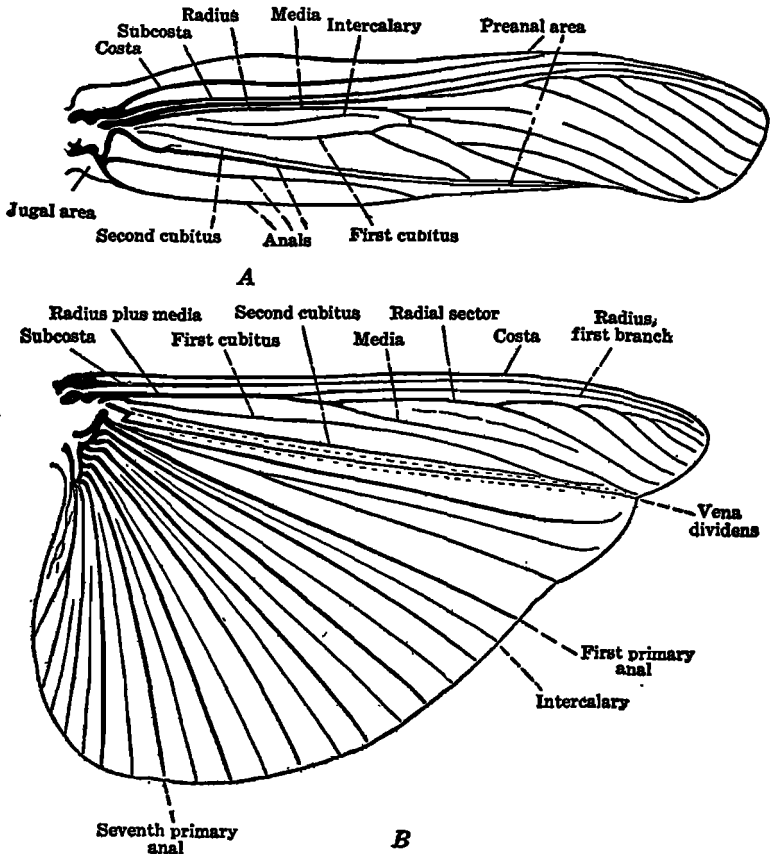


FIG. 294. — Carolina locust, *Dissosteira carolina*. Wings with names of principal wing veins. A, fore wing. B, hind wing. (After Snodgrass.)

three pads on the ventral surface, and the terminal segment bears a pair of *claws* between which is a fleshy lobe, the *pulvillus*.

*Wings* (Figs. 294, 295). — The wings of insects arise from the region between the tergum and pleurum as a double layer of hypodermis which secretes upper and lower cuticular surfaces. Between these are tracheæ around which spaces occur and the cuticula thickens; they later become the longitudinal wing veins.



The *veins* are of value in strengthening the wings. They differ in number and arrangement in different species of insects but are so constant in individuals of any one species that they are very useful for purposes of classification. The mesothoracic wings of the grasshopper, the *tegmina*, are leathery and not folded; they serve as covers for the metathoracic wings which lie beneath them. The latter are thin and folded like a fan.

*Abdomen.* — The number of segments in the abdomen of the embryo insect is eleven and each of these bears a pair of rudimen-

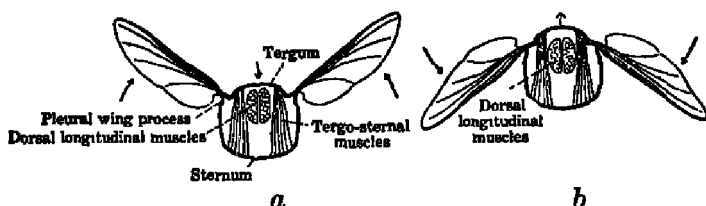


FIG. 295. — Movement of wings in flight. a, The wings are elevated on the pleural wing processes by the depression of the tergum due to the contraction of the tergo-sternal muscles. The hind margins of the wings are deflected. b, The wings are lowered by the elevation of the tergum due to the contraction of the dorsal, longitudinal muscles. Hind margins of wings elevated. (After Snodgrass.)

tary appendages. In the adult of most insects no appendages are present and the number of segments is usually reduced. In the grasshopper segment I is fused with the metathorax; it consists of a tergum only, on either side of which is an oval *tympenic membrane* covering an *auditory sac*. Segments IX and X have their terga partly fused together and their sterna completely fused. Segment XI consists of a tergum only; this forms the so-called *genitalia* consisting in the male of a *subgenital plate*, two *podical plates*, and two *cerci*, and in the female of two podical plates, two cerci, and three pairs of movable plates, which form the *ovipositor* or egg-laying apparatus.

*Internal anatomy* (Plate VI). — The systems of organs within the body of the insect lie in the body cavity, which is filled with blood and is a *hæmocœl* and not a *cœlom*. All of the systems characteristic of higher animals are represented.

*Muscular system* (Fig. 296). — The muscles are of the *striated* type, very soft and delicate but strong. The number present is very large. They are segmentally arranged in the abdomen but not in

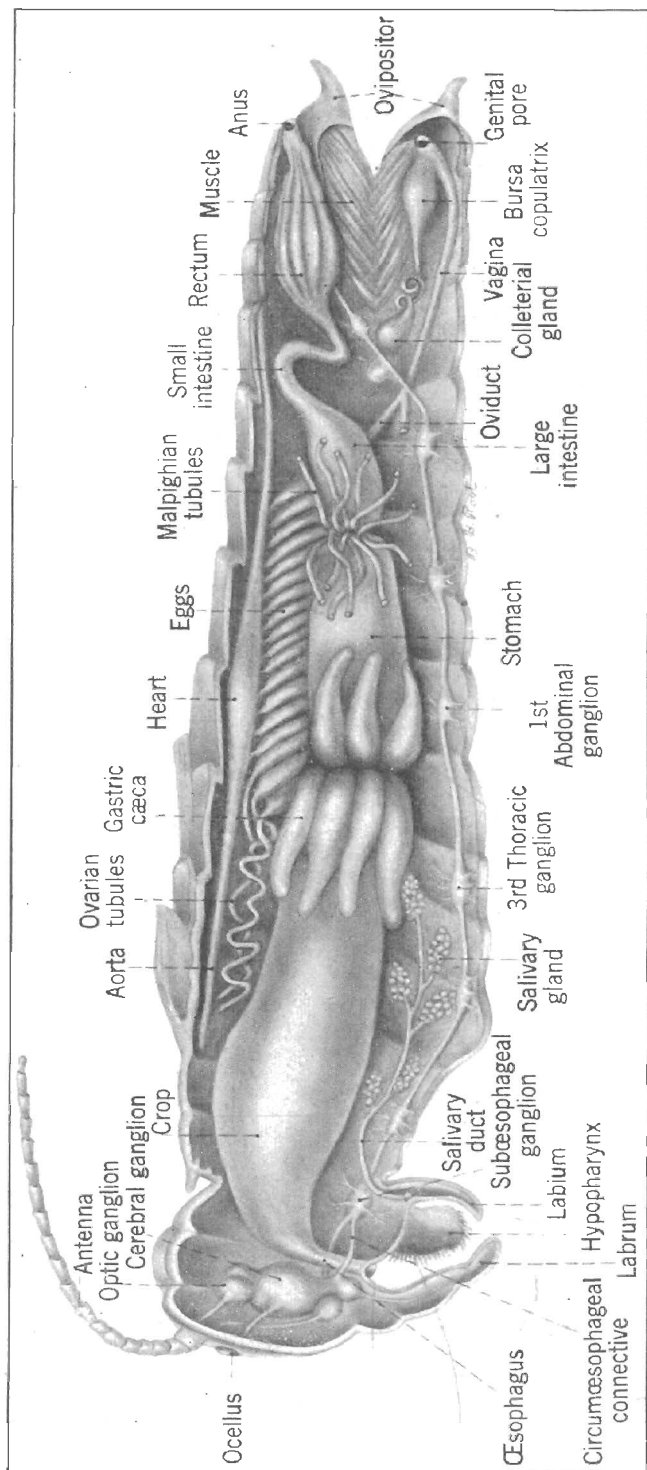


PLATE VI. Longitudinal section of a Grasshopper showing the internal organs. (Drawn by Barbara Bradley Root.)

the head and thorax. The most conspicuous muscles are those that move the mandibles, the wings, the metathoracic legs, and the ovipositor.

*Digestive system* (Plate VI). — The principal parts of the alimentary canal are the *fore gut*, *mid gut*, and *hind gut*. The fore gut consists of the *pharynx* in the head into which the *mouth* opens and on either side of which opens a *salivary gland*; next a tubular *oesophagus* which enlarges into a *crop* in the mesothoracic and metathoracic

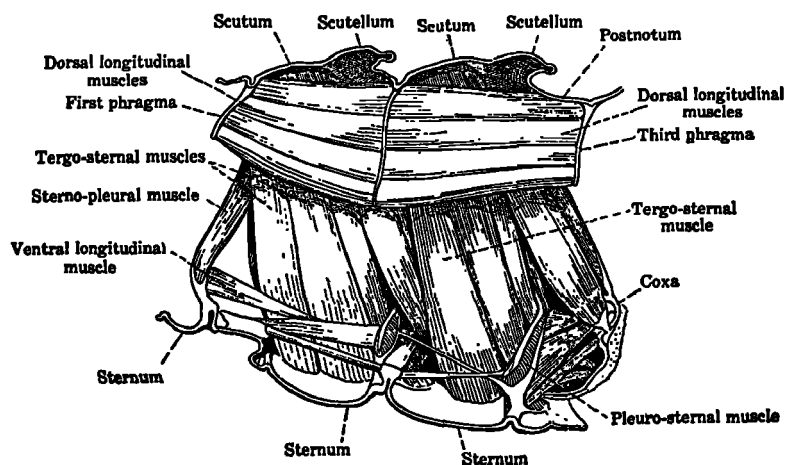


FIG. 296. — Carolina locust, *Dissosteira caolina*. General view of the musculature in the right half of the mesothorax and metathorax. The dorsal longitudinal muscles, by contraction, arch the tergal plates upward and thereby depress the wings; the tergo-sternal muscles depress the tergal plates, which indirectly elevate the wings. The other muscles are muscles of the legs and of the sterna. (After Snodgrass.)

segments; this leads into the *proventriculus* which is a grinding organ or *gizzard*. The mid gut which is the *ventriculus* or stomach, reaches posteriorly into the abdomen, and into it eight double, cone-shaped pouches, the *gastric ceca*, pour the digestive juices they secrete. The hind gut is made up of the *large intestine*, into the anterior end of which the delicate *Malpighian tubules* open; and the *small intestine*, which expands into the *rectum* and opens through the *anus*.

*Circulatory system* (Plate VI). — This is not a closed system of blood vessels as in vertebrates and some invertebrates but consists of a single tube located in the abdomen just under the body wall in the mid-dorsal line. The *heart* is divided into a row of

chambers into the base of each of which opens a pair of *ostia*. These *ostia* are closed by *valves* when the heart contracts. The *pericardial sinus* in which the heart lies is formed by a horizontal partition beneath it. At its anterior end the heart forms an *aorta*

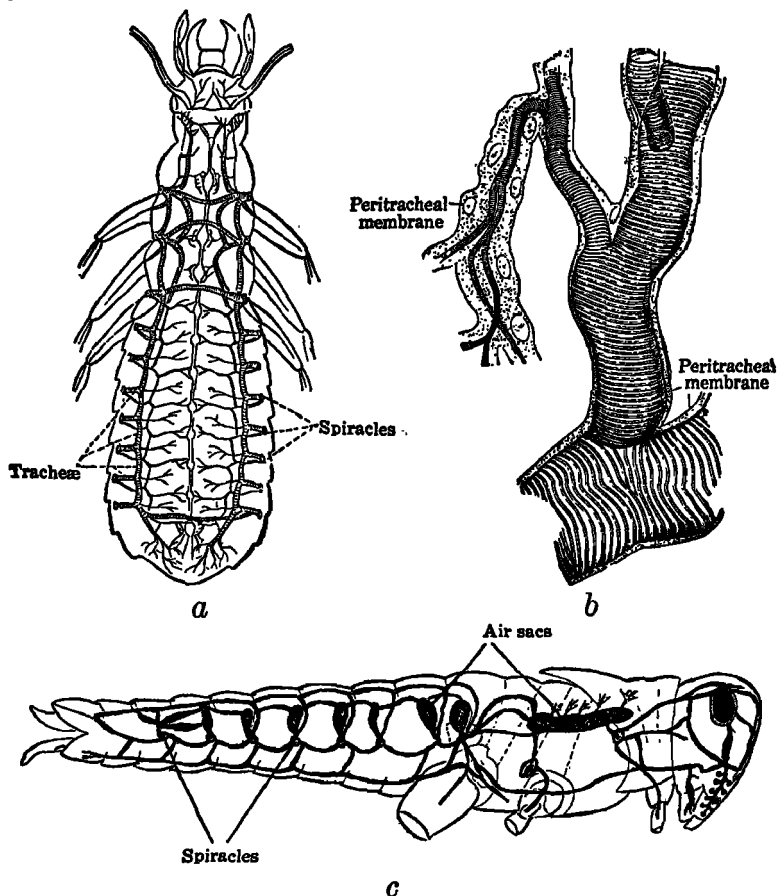


FIG. 297. — Respiratory system of insects. a, Diagram of tracheæ in the body of a beetle. b, Part of a trachea of a caterpillar. c, Tracheæ, air sacs and spiracles of a grasshopper. (a, after Kolbe; b, after Leydig; c, after Vinal.)

which opens into the body cavity or hæmocœl in the head region. Blood is forced anteriorly through the heart and aorta into the hæmocœl where it bathes all the organs. The blood carries nutriment but does not play a large part in respiration as it does in most of the METAZOA because of the highly developed tracheal

system. It consists of a *plasma* in which are suspended white blood cells, the *leucocytes*.

**Respiratory system** (Fig. 297). — The respiratory system consists of a network of ectodermal tubes, the *tracheæ*, that communicate with every part of the body. The tracheæ consist of a single layer of cells enclosing a chitinous lining, which, in the larger tubes, forms a *spiral thread* that prevents the trachea from collapsing. The tracheæ extend from the *spiracles* (Fig. 298) to a longitudinal trunk on either side of the body. The finest tracheæ, the *tracheoles*,

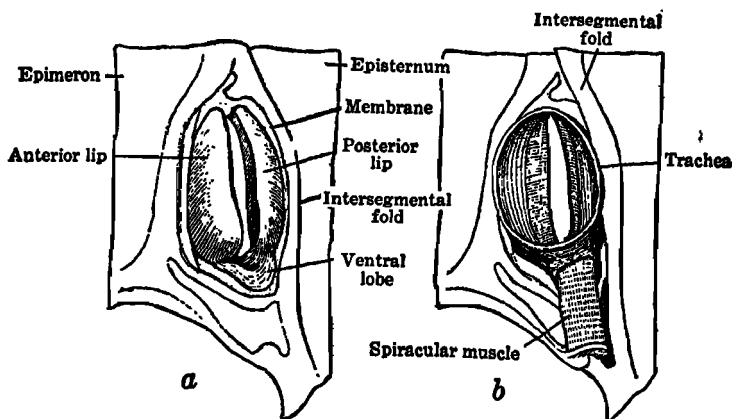


FIG. 298. — Carolina locust, *Dissosteira carolina*. a, Left spiracle of mesothoracic segment, outer view. b, Right spiracle of mesothoracic segment, inner view. (After Snodgrass.)

are connected directly with the tissue to which they supply oxygen and from which they carry away carbon dioxide, thus assuming the function performed in other animals by the circulatory system. In the grasshopper and certain other insects some of the tracheæ become expanded into thin-walled air sacs which are easily compressed and thus aid in the movement of air. Contraction and expansion of the abdomen draw air into and expel it from the tracheal system. In the grasshopper the first four pairs of spiracles are open at inspiration and closed at expiration, whereas the other six pairs are closed at inspiration and open at expiration.

**Excretory system.** — The organs of excretion are the *Malpighian tubules* that are coiled about in the hæmocœl and open into the anterior end of the hind gut. Uric acid has been found by microchemical tests in both the cells and lumen of these tubules.

*Nervous system* (Plate VI, Figs. 299, 300). — There is a *brain*, dorsally located in the head, consisting of three pairs of ganglia

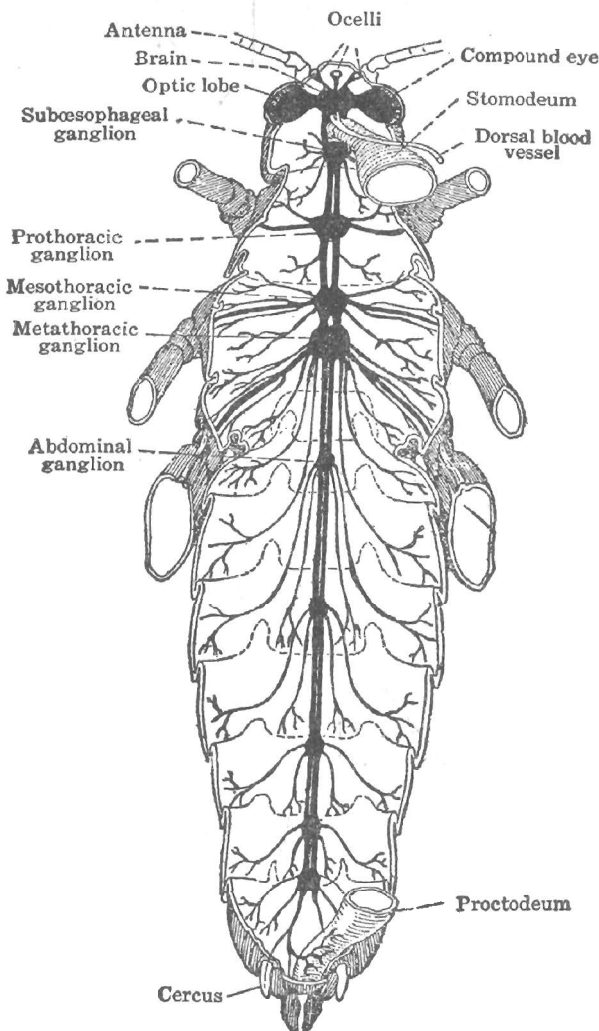


FIG. 299. — Carolina locust, *Dissosteira carolina*. Dorsal view showing nervous system. (After Snodgrass.)

fused together (Fig. 300). These ganglia supply the eyes, antennæ, and labrum. The brain is connected by a pair of *circum-æsoophageal connectives* with a *subesophageal ganglion*. This ganglion consists of the three anterior pairs of ganglia of the ventral nerve chain fused together, and supplies the mouth parts. The *ventral nerve chain* continues with a pair of large ganglia in each thoracic seg-

ment. The ganglia in the metathoracic segment are particularly large and represent the ganglia of this segment and of the first abdominal segment fused. Five pairs of ganglia are present in the abdomen. The pair in the second abdominal segment comprise the

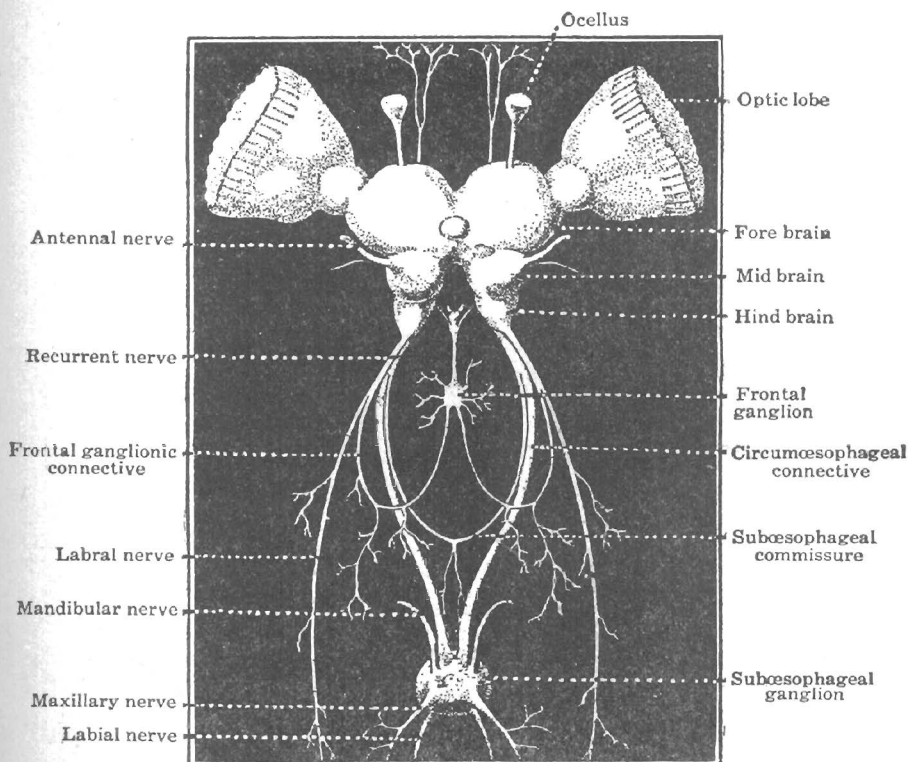


FIG. 300. — Carolina locust, *Dissosteira carolina*. The brain and subesophageal ganglion and their nerves, as seen after removal of the facial wall of the head. (After Snodgrass.)

pairs from the second and third abdominal somites fused together and the pair in the seventh segment represent the ganglia of the seventh to the eleventh somites combined. Connected with the brain are ganglia of the *sympathetic nervous system* which supplies the muscles of the alimentary canal and spiracles.

*Sense organs.* — Grasshoppers possess organs of sight, hearing, touch, taste, and smell. The *compound eye* and *ocellus* have already been noted. Vision by means of the compound eyes has been described in the crayfish (p. 385). The ocelli probably do not perceive objects but are merely organs of light perception. The

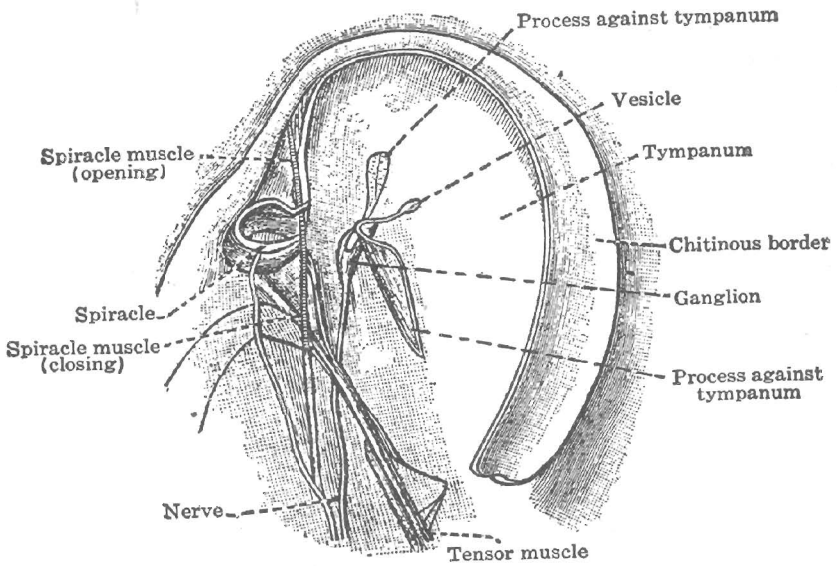


FIG. 301. — Auditory organ of a grasshopper. (After Graber.)

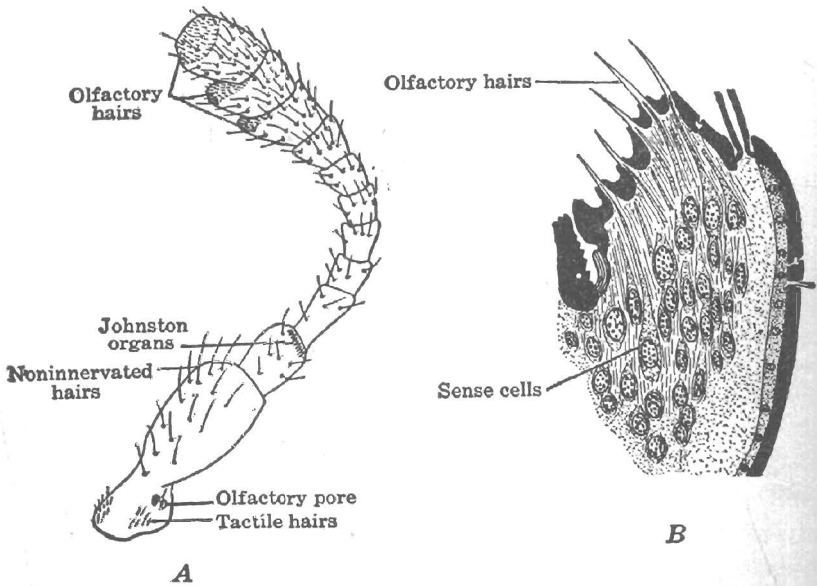


FIG. 302. — Sense organs of insects. Mexican bean weevil. A, Antenna, dorsal surface. B, Antenna, section through tenth segment. (After McIndoo.)



pair of *auditory organs* (Fig. 301) are located on the sides of the tergite of the first abdominal segment. They consist of a *tympanum* stretched within an almost circular chitinous ring. The *antennæ* (Figs. 302, 303) are supplied with the principal organs of smell. Organs of *taste* are located on the mouth parts. The hair-like

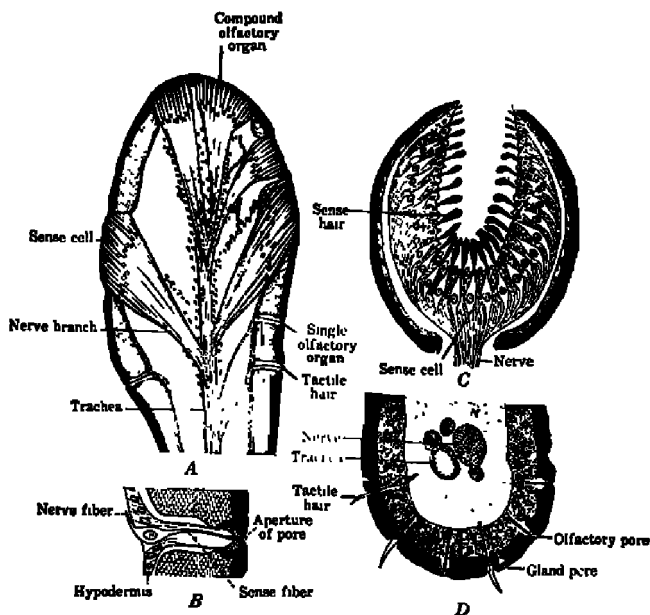


FIG. 303. — Sense organs of insects. A, Antenna of larva of a beetle, *Cotinis nitida*, longitudinal section of tip. B, Single olfactory organ from antenna of *Cotinis*, cross section. C, Sense organ, probably static or balancing, in labial palp of codling moth. D, Antenna of Mexican bean weevil, cross section of first segment. (After McIndoo.)

organs of *touch* are present on various parts of the body but particularly on the antennæ.

**Reproductive system.** — Female grasshoppers can easily be distinguished from males because of the presence of the *ovipositor* (Plate VI). In the female are two *ovaries*. Each consists of a number of filaments usually called *ovarian tubules* which, however, do not possess a lumen (Fig. 304). The *ovarian filaments* contain *oogonia* and *oocytes* arranged in a linear series, *nurse cells*, and other tissue cells. The oocytes grow as they proceed posteriorly down the

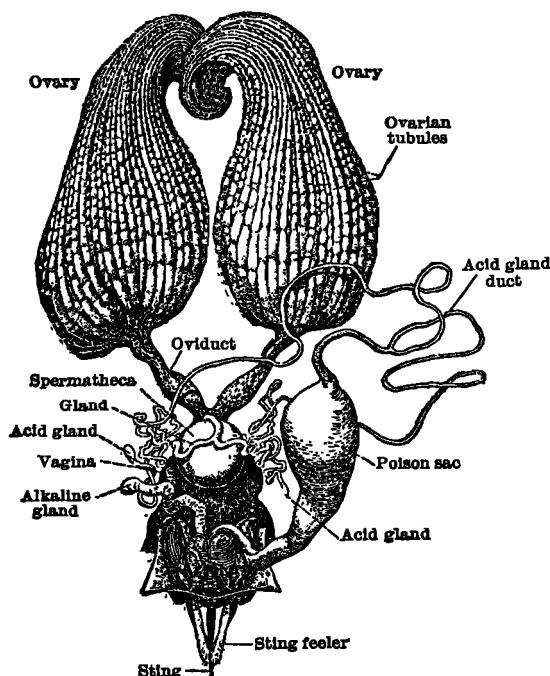


FIG. 304. — Reproductive organs, sting, and poison gland of queen honeybee. (From Snodgrass.)

filament, hence the filament becomes gradually larger toward the posterior end. The filaments of each ovary are attached posteriorly to an *oviduct* into which the eggs are discharged. The two oviducts unite to form a short *vagina* which leads to the *genital opening* between the plates of the *ovipositor*. A tubular *seminal receptacle*, or *spermatheca*, which opens dorsal to the vaginal pore, receives the *spermatozoa* during copulation and releases them when the eggs are fertilized. In the male are two *testes* in which *spermatozoa* develop (Fig. 305). These are discharged into a *vas deferens*. The two *vasa deferentia* unite to form an *ejaculatory duct* which opens on the dorsal surface of the *subgenital plate*. *Accessory glands* are present at the anterior end of the *ejaculatory duct* which apparently secrete a fluid that aids in the transfer of *spermatozoa* to the female.

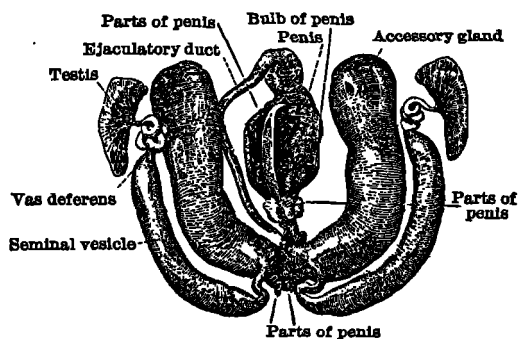


FIG. 305. — Reproductive organs of drone honeybee, dorsal view, natural position. (From Snodgrass.)

**Embryonic development and growth.** — The eggs are fertilized at the time they are deposited, by the entrance of spermatozoa through an opening in one end of the egg-shell called the *micropyle*. One sperm nucleus unites with the nucleus of the mature egg; a *blastoderm* is formed around the periphery of the egg from which an *embryo* develops. The young grasshopper that hatches from the egg is called a *nymph* (Fig. 306). It resembles its parent but has a large head compared with the rest of the body and lacks wings. As it grows its body becomes too large for the inflexible chitinous exoskeleton and the latter is shed periodically. Wings are gradually developed from wing buds and the adult condition is finally assumed. This type of development is called *direct metamorphosis* in contrast to the *indirect metamorphosis* of many insects which involves larval and pupal stages.

## (2) OTHER INSECTA

The INSECTA are air-breathing ARTHROPODA with bodies divided into head, thorax, and abdomen. The head bears one pair of antennæ and the thorax three pairs of legs and usually one or two pairs of wings in

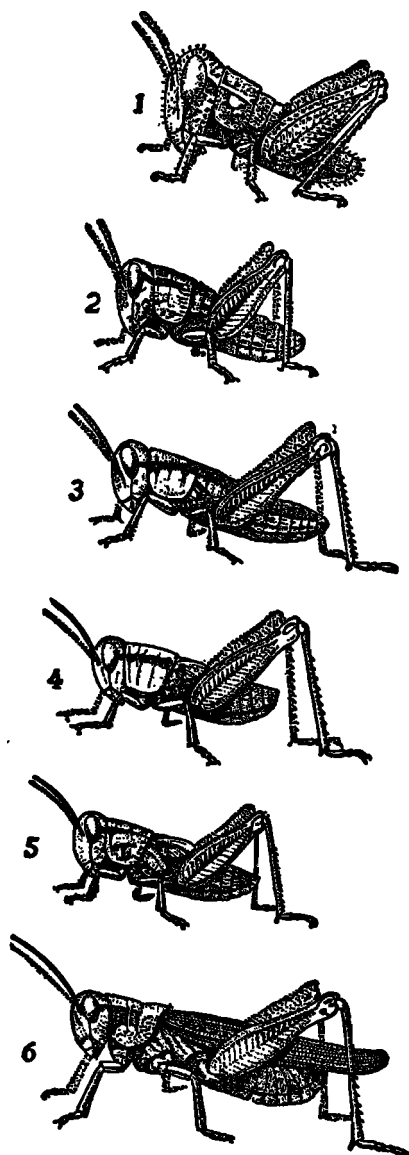


FIG. 306. — Metamorphosis of a grasshopper, *Melanoplus femurrubrum*, showing the five nymph stages, and the gradual growth of the wings. (From Packard, after Emerton.)

the adult stage. Insects are more numerous in species than all other animals taken together; over 650,000 species have been described and no doubt hundreds of thousands remain to be discovered. They live in almost every conceivable type of environment on land and in the water and their structure, habits, and life cycles are correspondingly modified. Nevertheless, it is possible to separate this vast assemblage into orders, families, etc., although there is no unanimity of opinion with respect to the number of these that should be recognized and to the names that should be applied to them. The following classification into orders is one commonly used by entomologists in this country.

Order 1. THYSANURA. Bristletails, Fish-moths, etc.

Order 2. COLLEMBOLA. Springtails.

Order 3. ORTHOPTERA. Cockroaches, Crickets, Grasshoppers, Locusts, etc.

Order 4. ISOPTERA. Termites or White Ants.

Order 5. NEUROPTERA. The Dobson, Aphid-lions, etc.

Order 6. EPHEMERIDA. Mayflies.

Order 7. ODONATA. Dragonflies.

Order 8. PLECOPTERA. Stoneflies.

Order 9. CORRODENTIA. Book-lice, etc.

Order 10. MALLOPHAGA. Bird-lice.

Order 11. EMBIIDINA. Embiids.

Order 12. THYSANOPTERA. Thrips.

Order 13. ANOPLURA. Sucking Lice.

Order 14. HEMIPTERA. Bugs.

Order 15. HOMOPTERA. Plant-lice, Scale-insects, etc.

Order 16. DERMAPTERA. Earwigs.

Order 17. COLEOPTERA. Beetles.

Order 18. STREPSIPTERA. Stylopids.

Order 19. MECOPTERA. Scorpion-flies, etc.

Order 20. TRICHOPTERA. Caddice-flies.

Order 21. LEPIDOPTERA. Moths, Skippers, and Butterflies.

Order 22. DIPTERA. Flies.

Order 23. SIPHONAPTERA. Fleas.

Order 24. HYMENOPTERA. Bees, Wasps, Ants, etc.

**Structural modifications.** — Before discussing the characteristics of these orders it seems desirable to point out certain structural modifications that may be encountered in the various groups.

The antennæ, mouth parts, legs, and wings are among the most interesting external features of insects.

*Wings.* — The mesothorax and metathorax bear each a pair of wings in most insects. Certain simple species (THYSANURA, Fig. 311) do not possess wings; others (lice and fleas, Figs. 325 and 355) have no wings, but this is because they are degenerate. The flies (DIPTERA, Fig. 347, *b*) have a pair of clubbed threads, called balancers or halteres, in place of the metathoracic wings. Attached to each thoracic segment is a pair of legs. Wings enable their owners to fly rapidly from place to place and thus to escape from enemies and to find a bountiful food supply. The success of insects in the struggle for existence is in part attributed to the presence of wings. Wings are outgrowths of the skin strengthened by a framework of chitinous tubes, called veins or nervures, which divide the wing into cells. The veins vary in distribution in different species, but are quite constant in individuals of any given species; they are consequently used to a considerable extent for purposes of classification. The principal longitudinal veins, as shown in figure 294, are the costa, subcosta, radius, media, cubitus, and anal. Cross veins frequently occur. Modifications come about by reduction or by addition. In the beetles (COLEOPTERA) the fore wings are sheath-like, and are called elytra. The fore wings of ORTHOPTERA (grasshoppers, etc.) are leathery and are known as tegmina.

*Legs.* — The legs of insects are used for various purposes and are highly modified for special functions, for example, those of the honeybee (Fig. 363). A typical leg consists of five parts, — coxa, trochanter, femur, tibia, and tarsus. The tarsus (Fig. 293) is usually composed of five segments and bears at the end a pair of claws, between which is a fleshy lobule, the pulvillus. Running insects possess long, slender legs (Fig. 334); the mantis has its fore legs fitted for grasping (Fig. 313); the hind legs of the grasshopper are used in leaping (Fig. 293); the fore legs of the mole cricket are modified for digging (Fig. 316, *c*); and the hind legs of the water beetle are fitted for swimming (Fig. 335, *a*). Many other types could be mentioned.

*Mouth parts.* — The mouth parts of insects are in most cases fitted either for biting (mandibulate) or sucking (suctorial). The grasshopper possesses typical mandibulate mouth parts (Fig. 291). The mandibles of insects that live on vegetation are adapted for

crushing; those of carnivorous species are usually sharp and pointed, being fitted for biting and piercing. Suctorial mouth parts are adapted for piercing the tissues of plants or animals and sucking juices. The mouth parts of the honeybee (Fig. 362)

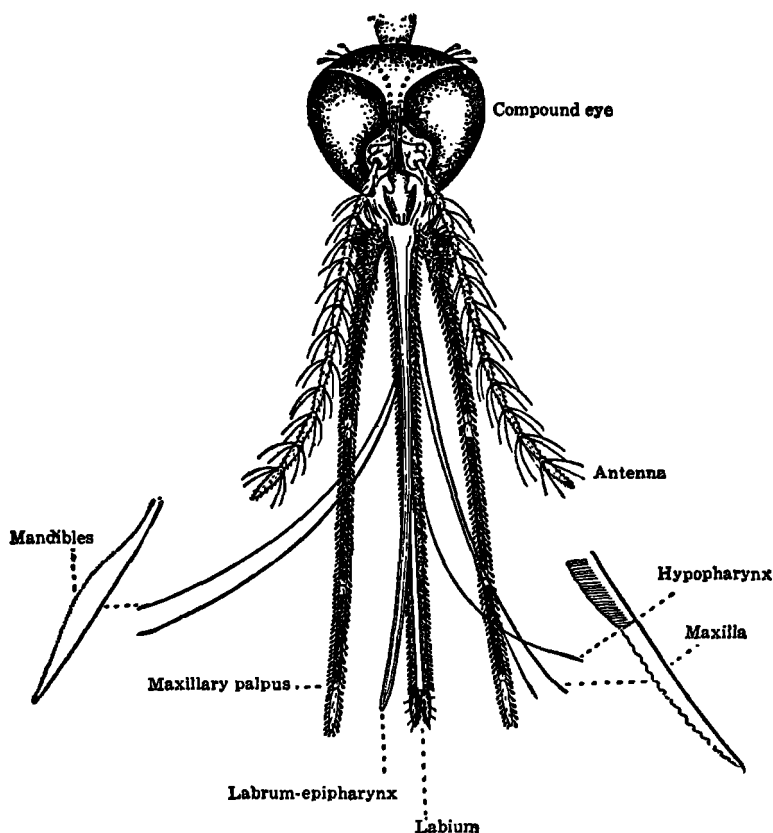


FIG. 307. — Sucking mouth parts of an anopheline mosquito (*A. costalis*), female. (After Carter.)

are suctorial, but highly modified. In the female mosquito (Fig. 307) the labrum and epipharynx combined form a sucking tube; the mandibles and maxillæ are piercing organs; the hypopharynx carries saliva; and the labium constitutes a sheath in which the other mouth parts lie when not in use. The proboscis of the butterflies and moths is a sucking tube formed by the maxillæ.

The mouth parts of insects are of considerable importance from

an economic standpoint, since insects that eat solid food can be destroyed by spraying the food with poisonous mixtures, whereas those that suck juices must be smothered with gases or have their spiracles closed with emulsion.

*Antennæ.* — The antennæ of insects are usually tactile, olfactory, or auditory in function. They differ widely in form and structure (Fig. 308). Often the antennæ of the male differ from those of the female.

*Alimentary canal.* — Of the internal organs of insects the alimentary canal and respiratory systems are of particular interest. The alimentary canal is modified according to the character of the food. An insect with mandibulate mouth parts (Plate VI) usually possesses (1) an oesophagus which is dilated to form a crop in which food is stored, (2) a muscular gizzard or proventriculus which strains the food and may aid in crushing it, (3) a stomach or ventriculus into which a number of glandular tubes (gastric ceca) pour digestive fluids, and (4) an intestine with urinary or Malpighian tubules at the anterior end. Suctorial insects, like the butterflies and moths (Fig.

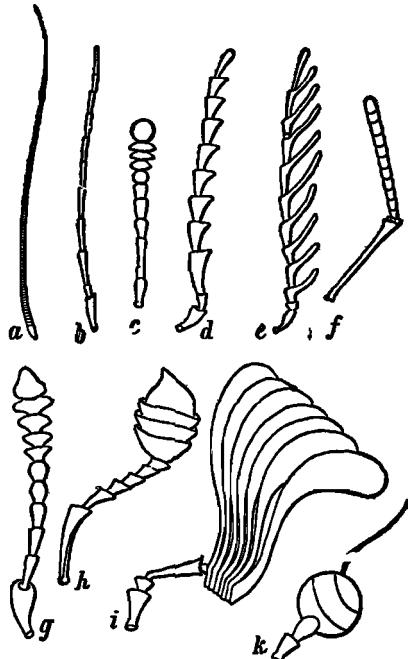


FIG. 308. — Different forms of antennæ of insects. a, bristle-like antenna of a grasshopper, *Locusta*; b, filiform, of a beetle, *Carabus*; c, moniliform, of a beetle, *Tenebrio*; d, dentate, of a beetle, *Elatér*; e, pectinate, of *Ctenicera*; f, crooked, of honeybee; g, club-shaped, of beetle, *Supha*; h, knobbed, of beetle, *Necrophorus*; i, lamellated, of beetle, *Melolontha*; k, with bristle, from fly, *Sargus*. (From Sedgwick, after Burmeister.)

309), are provided with a muscular pharynx which acts as a pumping organ and a sac for the storage of juices.

*Respiratory system.* — The respiratory system of insects is in general like that of the grasshopper (Fig. 297), but modifications occur in many species, especially in the larvæ of those that live in water. Aquatic larvæ, in many cases, do not have spiracles.

but get oxygen by means of thread-like or leaf-like cuticular outgrowths at the sides or posterior end of the body, termed tracheal gills (Fig. 321, *b*). Damsel-fly larvæ possess caudal tracheal gills, and the larvæ of dragon-flies take water into the rectum which is lined with papillæ abundantly supplied with tracheæ. The economic importance of a tracheal respiratory system has already been pointed out.

Other structural modifications, peculiar habits, and life cycles are noted in the discussion of the orders.

**Embryonic development** (Fig. 310). — The embryonic development of insects is a fascinating study. Eggs of the potato beetle,

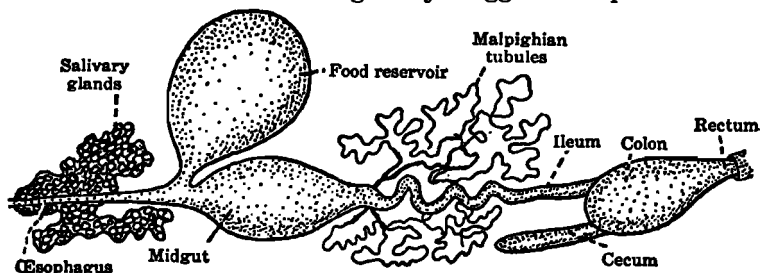


FIG. 309. — Alimentary canal of a sucking insect, a moth, *Sphinx*. (After Wagner, modified.)

for example, can easily be manipulated. They should be fixed in hot sublimate-acetic fluid and the shell picked off with needles. Sections can be cut after the eggs are embedded in paraffine and these as well as *in toto* preparations, can be stained with hæmalum. The fresh egg consists largely of yolk globules with a superficial layer of cytoplasm and thin cytoplasmic strands among the yolk (Fig. 310, *a*). The single fusion nucleus lies in a small island of cytoplasm. Nuclear division is not followed immediately by cell division but hundreds of nuclei are produced before cells are formed (*c*). Most of these nuclei migrate to the periphery and fuse with the superficial layer of cytoplasm; cell walls then appear and a blastoderm of a single layer of cells (*d*) covers the entire egg. The rest of the nuclei remain behind among the yolk globules which it is their duty to dissolve. The blastoderm thickens on one side of the egg forming the germ band in which appears a ventral groove (*e*). This groove is grown over by the amnioserosal fold and the germ band then becomes divided into segments. Appendages that are destined to become mouth parts and legs grow out from the



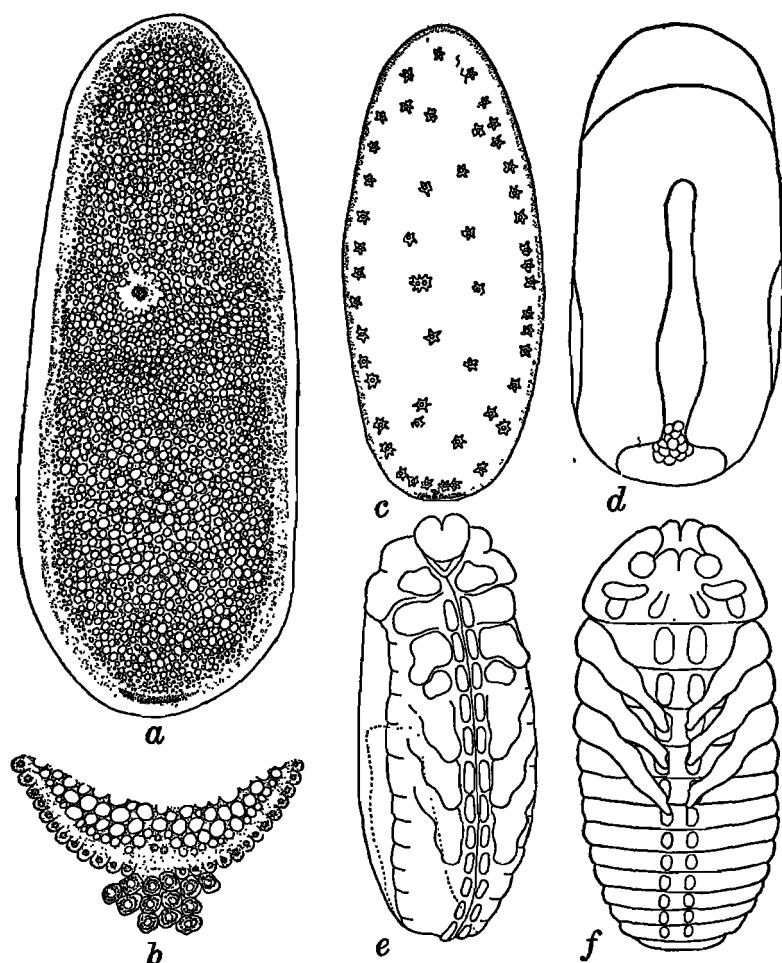


FIG. 310. — Embryonic development of a beetle. *a*, Longitudinal section of freshly laid egg showing fusion nucleus, yolk globules, peripheral layer of cytoplasm and, at the lower, posterior end, the pole disk of granular "germ-cell determinants." *b*, Blastoderm stage at end of twenty-four hours. The primitive germ cells have become extruded at the posterior end. *c*, Preblastoderm stage at end of twenty hours showing cleavage nuclei at periphery. *d*, Germ band with ventral groove; primitive germ cells near the posterior end. *e*, Embryo with segmentation in progress and appendages of head and thorax growing out. *f*, Older embryo with mouth parts and legs further developed. (From Hegner.)

cephalic and thoracic segments (*e, f*). The insect egg is very highly organized; certain parts of the potato-beetle egg are destined to produce certain definite parts of the embryo even before the blastoderm is formed as can be demonstrated by killing parts of the fresh egg with a hot needle and allowing the rest of the egg to develop. At the posterior end of the eggs of certain insects, especially DIPTERA, COLEOPTERA, and HYMENOPTERA, is a mass of granules that stain deeply with hæmatoxylin and appear to play an important part in the origin of the primordial germ cells; for this reason they are known as germ-cell determinants (*a*). These granules have been traced into the germ cells (*b*) and the latter have been followed from one generation to the next, illustrating very clearly the theory of the continuity of the germ plasm.

**Growth and metamorphosis.** — The eggs of insects are of various shapes and sizes. Some of them are colored; others are marked with polygonal areas or ridges. Three types of insects may be distinguished with respect to the method of their development; (1) ametabola, (2) hemimetabola, and (3) holometabola. The ametabolic insects are essentially like the adult, except in size, when they hatch from the egg; they develop to maturity without a metamorphosis. The THYSANURA (Fig. 311) are ametabolic.

The hemimetabolic insects hatch from the egg and develop into adults as in the grasshopper without passing through a true pupal period. Many of the species belonging to the hemimetabolic orders change considerably during the growth period, but are all more or less active throughout their development and are said to undergo direct or incomplete metamorphosis.

Holometabolic insects, such as the butterflies (Fig. 346), pass through both a larval and a pupal stage in their development. The majority of insects belong to this type.

**Order 1. THYSANURA.** — Bristletails (Fig. 311). Primitive wingless insects; ametabolic; chewing mouth parts; eleven abdominal segments; usually two or three long, filiform, segmented, caudal appendages; less than 20 species known from the United States. The pair of caudal appendages, or the outer two, if three are present, are cerci; the antennæ are long, filiform, and contain many segments; in some the compound eyes are degenerate or absent; in many the jaws are sunk into a cavity in the head; a few possess appendages of two segments, the styli, on the ventral

abdominal segments which may be remnants of legs of the many-legged ancestors of insects.

The silver-fish or fish-moth, *Lepisma saccharina* (Fig. 311, a), is a common species in houses, especially in the warmer parts of the country. It is covered with beautifully marked, shining scales,

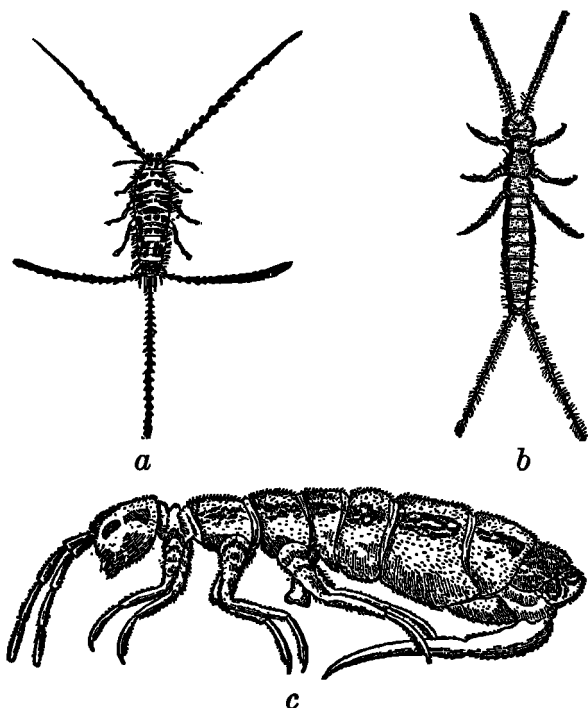


FIG. 311. — a, THYSANURA. *Lepisma saccharina*, the fish-moth. b, THYSANURA. *Campodea staphylinus*. c, COLLEMBOLA. Springtail. (a, from Wellhouse, after Kellogg; b, after Lubbock; c, after Miall.)

and often damages books, clothing, etc., because of its fondness for starch. *Campodea staphylinus* (Fig. 311, b) is a delicate, whitish species that lives under stones and leaves, and in rotten wood and other damp places. The fire-brat, *Thermobia domestica*, prefers a very warm environment such as the vicinity of stoves and fire-places. *Japyx* has pincer-like caudal appendages and *Machilis maratima* is a type that bears abdominal appendages.

Order 2. COLLEMBOLA. — Springtails (Fig. 311, c). Primitive wingless insects; ametabolic; chewing or sucking mouth parts;

four segments in the antennæ; usually no tracheæ; compound eyes absent; Malpighian tubules absent; tarsi absent; six abdominal segments; a springing organ present in most species on the ventral side of the fourth abdominal segment. The springing organ, or furcula, propels the insect into the air when it is released from a catch, the hamula, on the

third abdominal segment; mandibles are often overgrown by the cheeks; in some the mandibles and maxillæ are modified into piercing organs; on the ventral surface of

the first abdominal segment is a tube-like projection, or colophore, which holds the insects to the undersurface of an object with a sticky secretion from the labium.

COLLEMBOLA are very small insects, often microscopic in size. They are to be found in the crevices of bark, in moss, under stones,

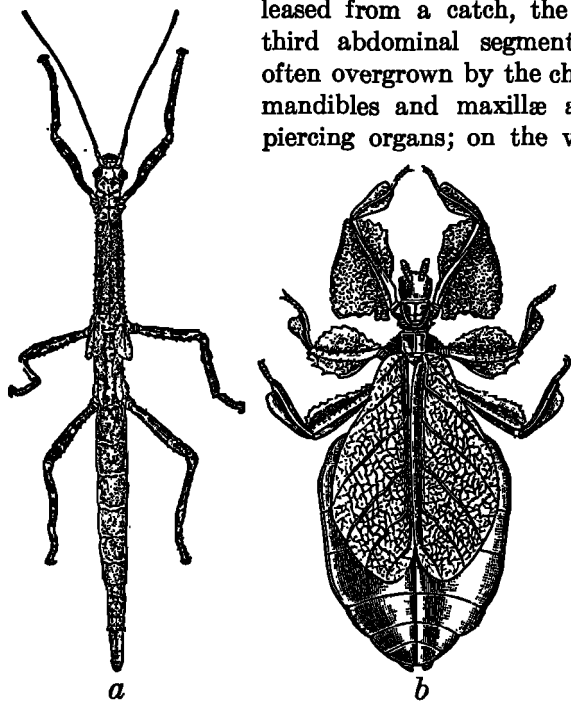


FIG. 312. — a, PHASMODÆ. *Diaperomera femorata*, the northern walking-stick. b, PHASMODÆ. *Phyllium scythe*, a leaf insect. (a, after Davenport; b, after Westwood.)

leaves, and wood where they feed on decaying matter. The snow-flea, *Archorutes nivicola*, sometimes occurs in winter on the snow in large numbers and is often a nuisance in maple sugar camps. The garden-flea, *Sminthurus hortensis*, may become a pest because of its fondness for young vegetables, such as cabbage, cucumbers, turnips, and squashes.

**Order 3. ORTHOPTERA.** — Grasshoppers, Crickets, Cockroaches, Katydid, Locusts, Walking Sticks, and Mantids. Holometabolic; chewing mouth parts; typically two pairs of wings, the fore wings

often thickened and parchment-like and called tegmina (singular, tegmen), the hind wings folded like a fan beneath the fore wings; in some, wings are vestigial or absent. The six families in this order may be grouped into the CURSORIA (PHASMIDÆ, MANTIDÆ, and BLATTIDÆ) with metathoracic legs adapted for walking or running and the SALTATORIA (TETTIGONIDÆ, GRILLIDÆ, and LOCUSTIDÆ) with metathoracic legs adapted for leaping.

Family 1. PHASMIDÆ (Fig. 312). — Walking Sticks and Leaf Insects. These are herbivorous insects. Some of them are wingless and have a slender body, and long legs and antennæ, which give them a stick-like appearance. They are not active and move slowly. Their resemblance to the twigs on which they rest and



FIG. 313. — MANTIDÆ. *Stagmomantis carolina*, the praying mantis. (After Packard.)

their habit of feigning death, furnish an example of mimicry. *Diapheromera femorata* (Fig. 312, *a*) is the common walking stick of the northern United States. *Aplopus mayeri* is our only winged phasmid; it occurs in Florida. In the tropics are many species with expansions of the abdomen and leg segments and with wings that give them a close resemblance to leaves.

Family 2. MANTIDÆ (Fig. 313). — Mantids. The mantids are carnivorous, feeding on other insects. The prothorax is much elongated and the prothoracic legs are modified as grasping organs. Spines are present on the tibiae and femora and the former can be bent back so as to hold any insect grasped by them. As they lie in wait for their prey, the fore legs are raised in an attitude of prayer, hence the common name, praying mantis. *Stagmomantis carolina* (Fig. 313) is a species that occurs as far north as Maryland and southern Indiana. Other species live in the southern United States; many of those that live in the tropics have wings that resemble the leaves of plants in shape and color.

Family 3. **BLATTIDÆ** (Fig. 314). — Cockroaches. These are omnivorous insects with dorso-ventrally flattened body, head bent down beneath the thorax, long antennæ, and legs adapted for running. They are often a nuisance in houses. In nature, they live under stones, sticks, and other objects. The eggs are enclosed in capsules, the oothecæ. Some forms are wingless. Three species

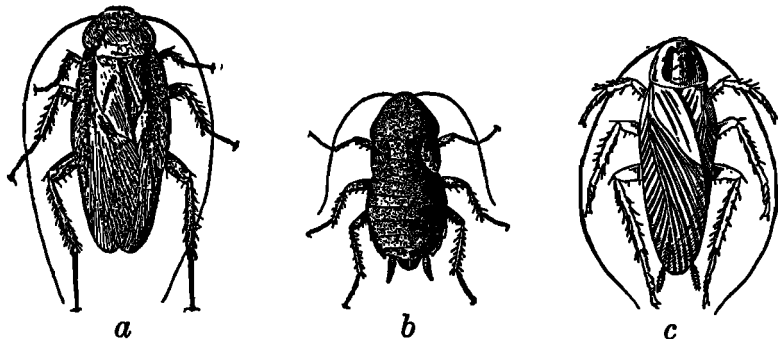


FIG. 314. — **BLATTIDÆ**. a, *Periplaneta americana*, the American cockroach. b, *Blatta orientalis*, the "black-beetle"; nymph. c, *Blattella germanica*, the "croton-bug." (a, b, from Herrick; c, from Essig.)

that occur in the United States are *Periplaneta americana* (Fig. 314, a), the American cockroach; *Blattella germanica* (c), the croton-bug, which was introduced from Europe, and *Blatta orientalis* (b), the oriental cockroach, which probably reached America from Asia.

Family 4. **TETTIGONIDÆ** (Fig. 315). — Long-horned Grasshoppers. The antennæ of this group are very long and slender; the tarsi have four segments; the ovipositor is long and sword-shaped; the body is often colored green and is hence inconspicuous; and the auditory organs are located in the base of the tibiæ of the prothoracic legs. In many species the males have certain veins and cells of each wing-cover near the base so modified that when rubbed together they vibrate and produce a sound. The katydid, *Pterophylla camellifolia*, owes its name to its rasping call notes. Meadow grasshoppers, such as *Conocephalus*, are light-green forms that live among the grass in meadows. Certain cricket-like species, such as *Ceuthophilus*, are known as cave crickets or camel crickets; they live in dark, moist places in caves, cellars, under stones and wood, etc. The shield-backed grasshoppers are mostly wingless or nearly wingless species, such as the genus *Atlanticus*, and also resemble

crickets somewhat in appearance. They live in grassy fields or open woods.

Family 5. GRYLLIDÆ (Fig. 316). — Crickets. Most crickets have long antennæ, metathoracic legs for leaping, and a spear-shaped ovipositor. The males have a highly differentiated stridulating apparatus consisting of a file on the base of one tegmen and a scraper on the other. When the wings are held up over the body,

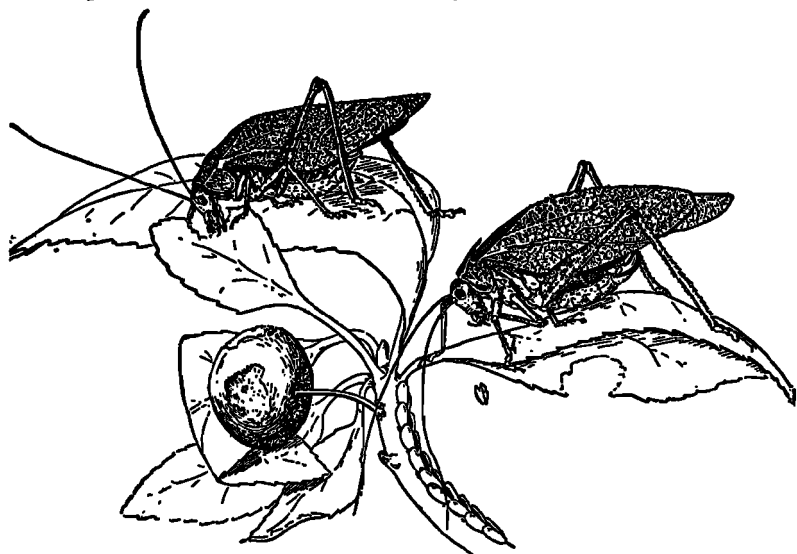


FIG. 315. — TETTIGONIIDÆ. *Microcentrum rhombifolium*, a katydid; male, female, eggs along stem and injury to leaf and apple. (From Essig.)

the file is rubbed over the scraper as the wings vibrate and produce the characteristic chirp. Many of the tree-crickets are light green in color and live in trees. *Oecanthus niveus*, the snowy tree-cricket, is a common species. When a number of individuals are close together they chirp in unison. Field crickets are brown in color and are abundant in fields where they usually hide in the daytime under stones, etc., or in burrows in the earth but are active at night. Some of them enter houses including the house cricket of Europe, *Gryllus domesticus* (Fig. 316, a), which has been introduced into the northeastern United States. Mole-crickets (*Gryllotalpa*) are likewise nocturnal. They burrow in the ground and have the tibiae of the prothoracic legs broadened and provided with stout spines well adapted for digging.

Family 6. LOCUSTIDÆ (Fig. 289). — Locus' s or Short-horned Grasshoppers. Here the antennæ are not as long as the body and consist of less than 26 segments; the ovipositor is composed of several short plates; and the first abdominal segment bears a tympanum on either side. Locusts are vegetarians and often cause great damage to crops. The males produce sounds either by rubbing the row of spines on the inner surface of the femur of the meta-thoracic leg against the outer surface of the tegmina, or while flying, by rubbing the upper surface of the anterior edge of the hind wings against the undersurface of the tegmina. Common species are the red-legged locust, *Melanoplus femur-rubrum*, the

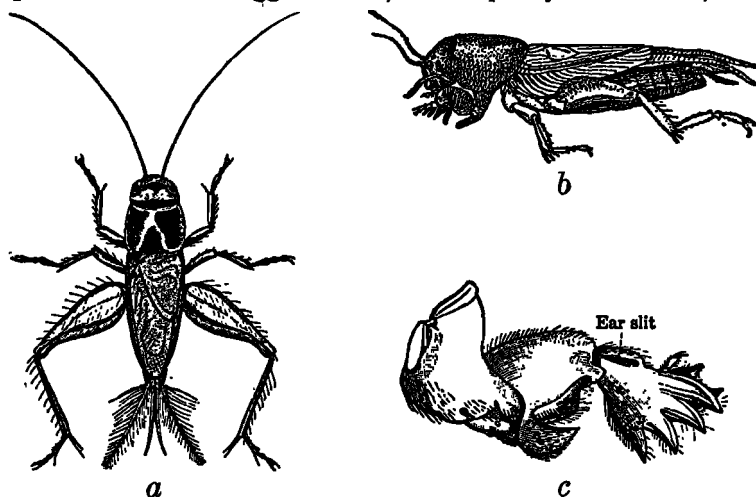


FIG. 316. — GRYLLIDÆ. a, *Gryllus domesticus*, the house cricket. b, *Scapteriscus didactylus*, a mole cricket. c, Leg of a mole cricket, showing ear slit. (a, from Herrick; b, after Barrett; c, from Sedgwick.)

Carolina locust, *Dissosteira carolina*, the clouded locust, *Encop-  
tolophus sordidus*, the American locust, *Schistocera americana*, the  
lubber grasshopper, *Brachystola magna*, and the Rocky Mountain  
locust, *Melanoplus spretus*, which has been so destructive to crops  
in Kansas, Iowa, and Nebraska during its migrations. The locusts  
that were responsible for the plagues of the Pharaohs belonged to  
this family. Also in this group are certain small active pigmy lo-  
custs, such as *Acrydium*, characterized by the presence of a pron-  
otum that extends back over the dorsal surface of the abdomen,  
sometimes beyond the posterior end of the body.



**Order 4. ISOPTERA** (Fig. 317). — Termites or White Ants. Hemimetabolic; chewing mouth parts; two pairs of long, narrow wings laid flat on the back when at rest, or wingless; abdomen joined directly to thorax. These social insects live in colonies much like ants, and are especially abundant in the tropics. They live mostly under cover and the cuticula is light in color and delicate. The adult sexual males and females after their nuptial flight shed their wings near the base where there is a transverse,

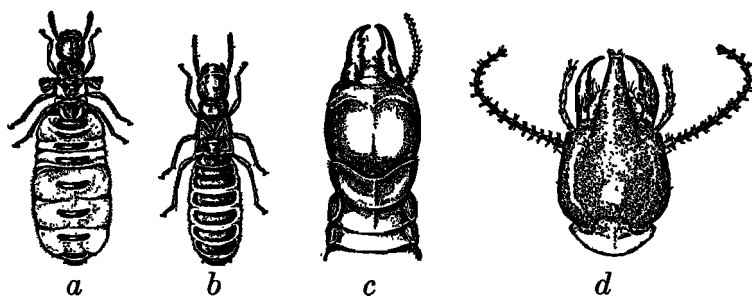


FIG. 317. — ISOPTERA; termites. a, *Reticulitermes flavipes*. Mature egg-laying female or queen with abdomen distended. b, *R. flavipes*. Mature male. c, *Kalotermes occidentalis*. Anterior end of soldier showing large mandibles, and wing pads. d, *Armitermes intermedius*. Anterior end of soldier showing large biting mandibles, and nasus. (After Snyder.)

humeral suture. The castes of termites are more numerous than those of other social insects, such as the bees, wasps, and ants. The species differ with respect to the number of castes present, but each caste contains both males and females. Four castes are usually present: (1) the first reproductive caste, with wings which are shed after the nuptial flight; these are known as king and queen or the primary royal pair; (2) the second reproductive caste, sexually mature but nymphal in form, and known as substitute or complemental king and queen; (3) sterile workers, which carry on the various activities necessary for the maintenance of the colony, are wingless and usually blind; and (4) sterile soldiers, which are supposed to protect the colony, are wingless, and possess very large heads and mandibles. *Reticulitermes flavipes* is the common species in the northeastern United States. As in many other species, its food consists of dead wood, and it works in the dark, hence, the inside of timbers in buildings are often eaten away without evidence of damage until nothing but a shell remains. Huge

nests in the form of mounds over ten feet in height are built by certain species that live in the tropics. Termite nests are often inhabited by other species of insects; these are called termitophiles. Over one hundred species of termitophiles have been recorded. The relation between termites and their intestinal protozoa has already been described (p. 52).

**Order 5. NEUROPTERA** (Fig. 318). — The Dobson, Aphis-lions, Ant-lions, and others. Holometabolic; chewing mouth parts; four similar membranous wings, usually with many veins and cross veins; no abdominal cerci; larvæ carnivorous, some with suctorial mouth parts; tracheal gills usually present on larvæ that are aquatic. Thirteen of the twenty families have representatives in

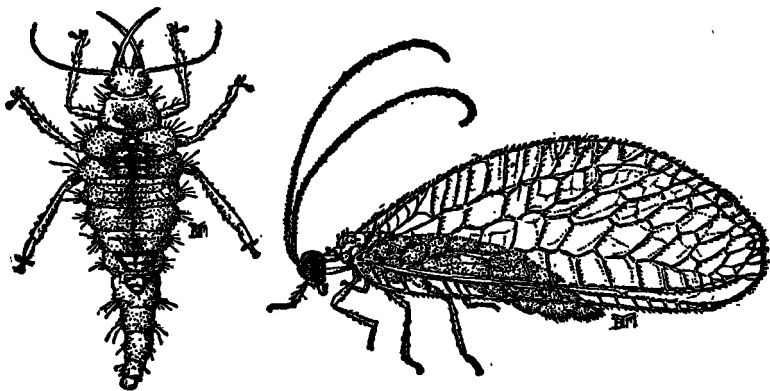


FIG. 318. — NEUROPTERA. *Chrysopa californica*, a lace-wing-fly, larva and adult. (After Quayle.)

North America. Among the interesting or common species are the horned corydalus, *Corydalus cornutus*, of the family SIALIDÆ, whose larvæ are used for bait by fishermen and known as dobsons or hellgramites; the lace-wing-flies of the family CHRYSOPIDÆ (Fig. 318), such as *Chrysopa oculata*, whose larvæ are called aphid-lions because they feed on aphids; and the ant-lions, larvæ of members of the family MYRMELEONIDÆ, such as *Myrmeleon immaculatus*, which live at the bottom of a small pit in the sand and grasp with their strong suctorial jaws any insects that may chance to slide down the precipitous sides.

**Order 6. EPHEMERIDA** (Fig. 319). — Mayflies. Hemimetabolic; mouth parts of adult, vestigial; two pairs of membranous, triangular wings, the fore wings larger than the hind wings; caudal

filament and cerci very long. The single family, EPHEMERIDÆ, belonging to this order contains a number of species of delicate insects known as mayflies. The larvæ live in the water and breathe by means of tracheal gills (Fig. 319, b), usually located in a row on either side of the abdomen; these are outgrowths of the integument containing tracheal branches. Oxygen is obtained by them from the water. The adults live only a short time, hence the derivation of the name EPHEMERIDA from the Greek word *ephemeros*, meaning lasting but a day. Frequently large numbers of adults emerge from the water at about the same time and huge swarms of them suddenly appear; for example, *Ephemera simulans*, around the lakes of the northern United States. The adults when they leave the water are called subimagos, because they molt within a few minutes to twenty-four hours after they acquire functional wings; they are the only insects that molt in the adult stage.

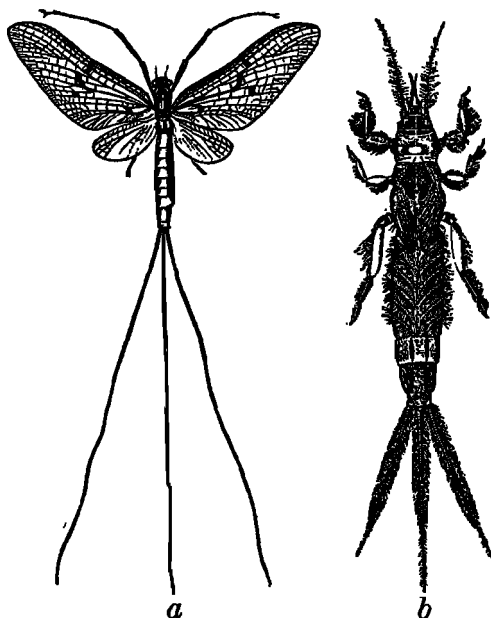


FIG. 319. — EPHEMERIDA. *Ephemera*, a mayfly. a, adult; b, nymph. (From Kennedy.)

**Order 7. Odonata** (Figs. 320, 321). — Dragon-flies and Damselflies. Hemimetabolic; chewing mouth parts; two pairs of membranous wings, the hind wings as large as or larger than the fore wings; large compound eyes; small antennæ; nymphs aquatic; both nymphs and adults, predacious. The dragon-flies (suborder ANISOPTERA, Fig. 320) belong to two families, the *ÆSCHNIDÆ* and *LIBELLULIDÆ*. In the adult, the wings are usually held in a horizontal position when at rest and the eyes may be made up of larger facets above and smaller ones below. The nymphs breath

by means of rectal gills, which line the enlarged posterior end of the alimentary canal, and extract oxygen from the water that is drawn in and expelled from this cavity. The labium of the larva is much

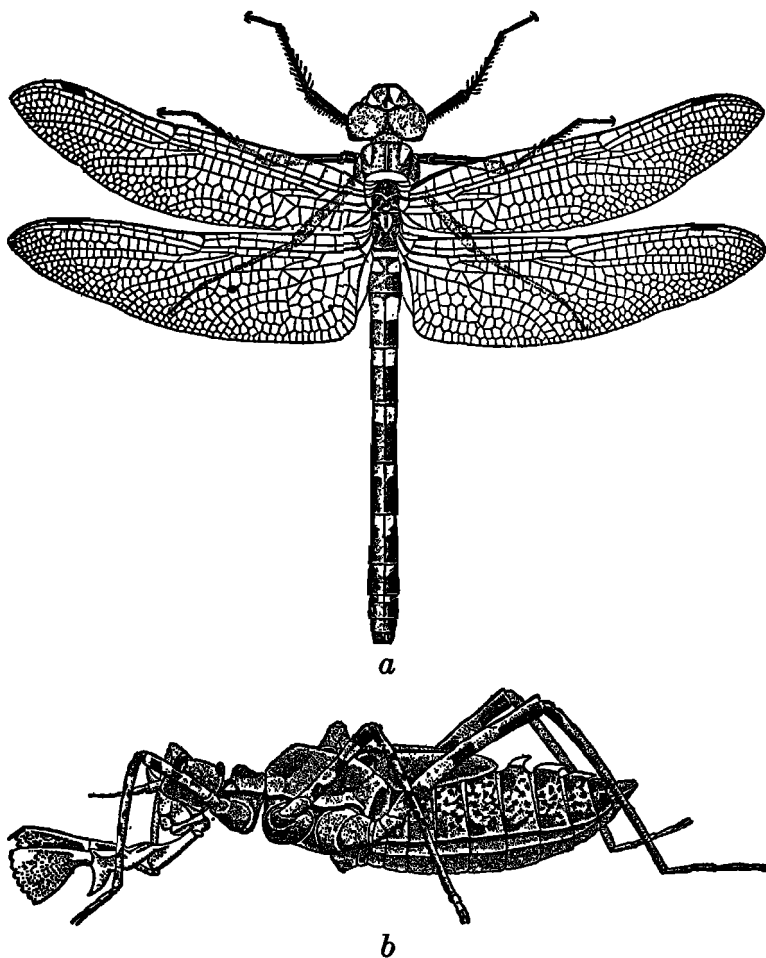


FIG. 320. — Odonata. *Macromia magnifica*, a dragon-fly. a, adult; b, nymph. (From Kennedy.)

elongated and can be extended rapidly from its folded resting position beneath the head so as to impale its prey on the hooks at the end. *Anax junius* is a common, widely spread species of the family *ÆSCHNIDÆ*. The damsel-flies (suborder *ZYGOPTERA*, Fig.

321) are also separated into two families, the AGRIONIDÆ and the CENAGRIONIDÆ. In the adults, the wings are parallel with the abdomen when at rest, and are delicate compared with those of the dragon-flies. *Agrion maculatum* is a common, dark-colored species partial to streams in woods.

Order 8. PLECOPTERA (Fig. 322). — Stone-flies. Hemimetabolic; chewing mouth parts, often undeveloped in adults; two pairs of wings, the hind wings usually larger and folded beneath the fore wings; tarsus with three segments; nymphs aquatic, usually in

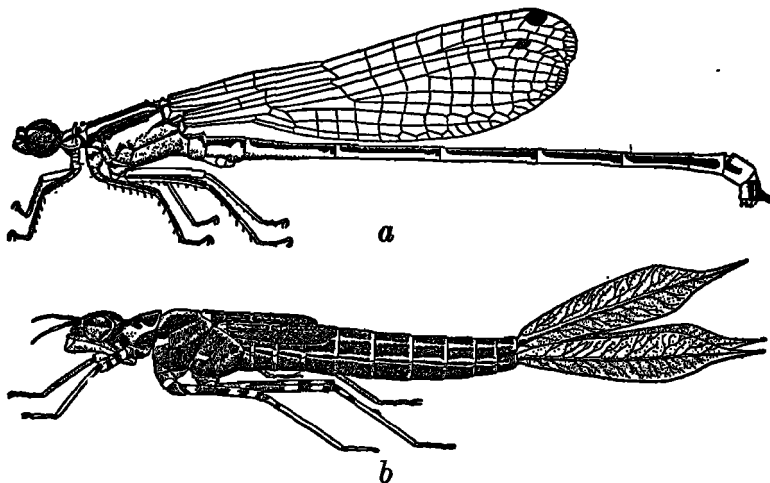


FIG. 321. — ODONATA. *Ischnura cervula*, a damsel-fly. a, adult, male; b, nymph. (From Kennedy.)

flowing water under stones, often with tufts of tracheal gills. Four of the seven families have representatives in this country. *Allocapnia pygma* is a common species that may appear on the snow in winter and hence is known as the snow-fly. *Tænipteryx pacifica*, the salmon fly, is a pest in parts of the state of Washington because it destroys the buds of fruit trees.

Order 9. CORRODENTIA (Fig. 323, a). — Psocids and Book-lice. Hemimetabolic; chewing mouth parts; wingless or with two pairs of membranous wings that have few, prominent veins, the fore wings larger than the hind wings; wings, when at rest, held over body like the sides of a roof. Two families occur in the United States. The family PSOCIDÆ contains winged species that live on trees, feeding on dry vegetable matter. They are known as psocids

or bark-lice. The ATROPIDÆ are wingless and called book-lice because they are often observed in old books. *Troctes divinatorius*

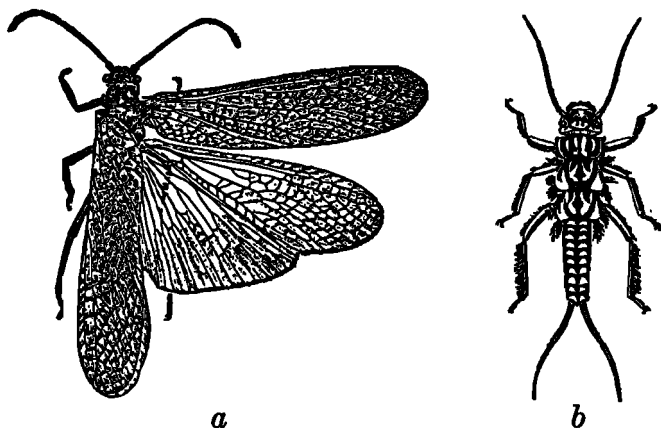


FIG. 322. — PLECOPTERA. Stone-fly. a, adult; b, nymph showing tracheal gills. (a, after Comstock; b, after Sharp.)

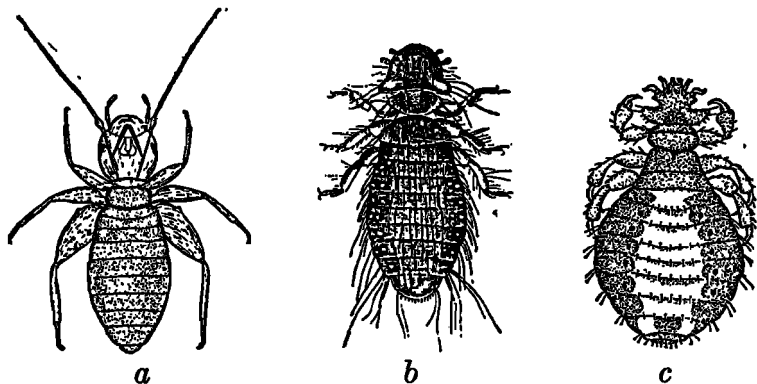


FIG. 323. — a, CORRODENTIA. *Troctes divinatorius*, a book-louse or "death-watch." b, MALLOPHAGA. *Menopon pallidum*, a chicken louse. c, MALLOPHAGA. *Gyropus ovalis*, a guinea-pig louse. (a, from Herrick; b, after Piaget; c, after Osborn.)

is a species of this type which feeds on the starch in bookbindings (Fig. 323, a).

Order 10. MALLOPHAGA (Fig. 323, b, c). — Bird-lice. Ametabolic; chewing mouth parts; wings absent; eyes degenerate. The *Mallophaga* are ectoparasites of birds and, less frequently, of mammals. They feed on hair, feathers, and dermal scales. Those that live

on mammals usually possess tarsi with one claw adapted for grasping hair; whereas those that live on birds possess tarsi with two claws which aid them in moving among feathers. Representative species are *Menopon pallidum* (Fig. 323, b), the common chicken louse, *Goniodes styliifer*, the turkey louse, and *Trichodectes scalaris* that lives on cattle.

**Order 11. EMBIIDINA** (Fig. 324, a). — Embiids. Hemimetabolic; chewing mouth parts; wingless or with two pairs of delicate, membranous wings, containing few veins, and folded on the back when at rest; and cerci of two segments present. The males are usually winged and the

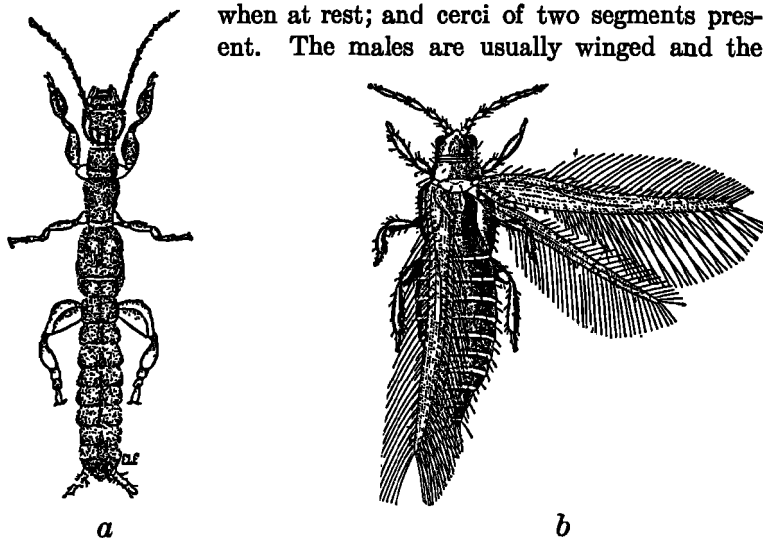


FIG. 324. — a, EMBIIDINA. *Embia californica*, the California embiid. b, THYSANOPTERA. A thrips. (a, from Essig; b, from Moulton.)

females wingless. Embiids live in warm countries and have been reported from California, Texas, and Florida. They live under stones and other objects in tunnels formed of silk produced by tarsal glands, and some of the 60 or more species known are gregarious. *Embia texana* is a species discovered in Texas, and *E. californica* (Fig. 324, a) a species from California.

**Order 12. THYSANOPTERA** (Fig. 324, b). — Thrips. Hemimetabolic; piercing mouth parts; wingless or with two pairs of similar, long, narrow, membranous wings with few or no veins, and fringed with long hairs; prothorax large and free; tarsi with two or three segments terminating in a bladder-like, protrusible vesicle. Some

species of thrips are injurious to cultivated plants; others are carnivorous and feed on aphids, red spiders, etc. Two suborders are recognized. The TEREBRANTIA contains many injurious species the females of which lay their eggs in the tissues of plants with their

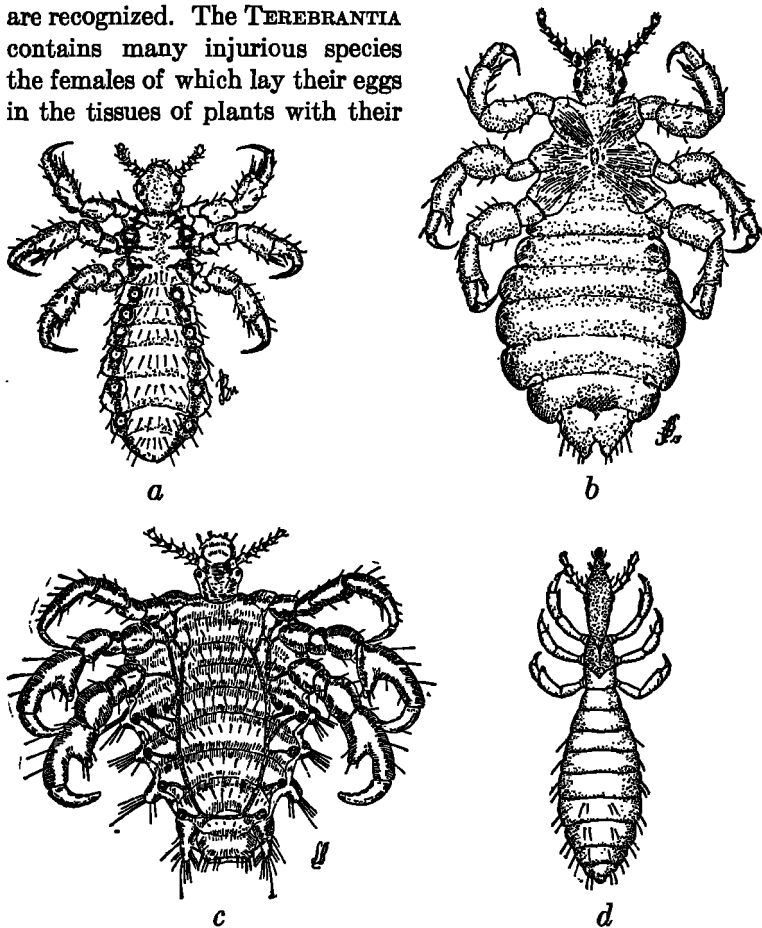


FIG. 325. — ANOPLURA. a, *Pediculus capitis*, the human head louse. b, *Pediculus corporis*, the human body louse. c, *Phthirus pubis*, the human crab louse. d, *Haematopinus vituli*, the long-nosed ox louse. (a-c, from Herrick; d, after Osborn.)

saw-like ovipositors. Here belong the onion thrips, *Thrips tabaci*, the greenhouse thrips, *Heliothrips hæmorrhoidalis*, the pear thrips, *Tæniothrips inconsequens*, the strawberry thrips, *Frankliniella tritici*, and many others. The members of the suborder TUBULIFERA are not so injurious and the females do not possess a saw-



like ovipositor. Common species are the mullein thrips, *Neoheggeria verbasce*, and the camphor thrips, *Cryptothrips floridensis*.

**Order 13. ANOPLURA** (Fig. 325). — Sucking Lice. Ametabolic; piercing and sucking mouth parts; wingless; ectoparasites on mammals; eyes poorly developed or absent; tarsus with one seg-

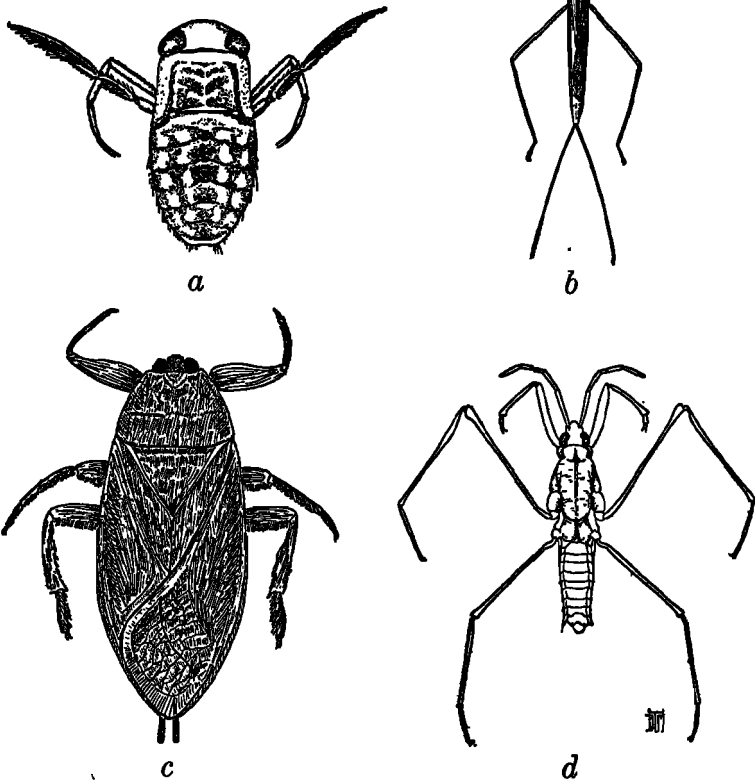


FIG. 326. — HEMIPTERA. a, CORIXIDÆ. *Artocoriza alternata*, a water boatman. b, NEPIDÆ. *Ranatra linearis*, a water scorpion. c, BELOSTOMATIDÆ. *Lethocerus*, an electric light bug. d, GERRIDÆ. *Gerris remigis*, a water strider. (a, after Hungerford; b, after Sharp; c, from Herrick; d, after Woodworth.)

ment bearing a single, large, curved claw adapted for clinging to the hair of the host. The eggs of ANOPLURA are fastened with a glue-like substance to the hairs of the host and are known as nits. Three species occur on man, the head louse, *Pediculus*

*capitis* (Fig. 325, *a*), the crab louse, *Phthirus pubis* (*c*), and the body louse, *Pediculus corporis* (*b*). Several important diseases are transmitted from man to man by the body louse, including typhus, relapsing, and trench fevers. Among the ANOPLURA of domestic animals are *Linognathus piliferus*, the dog louse; *Hæmatopinus suis*, the hog louse; and *Hæmatopinus vituli*, the ox louse.

**Order 14. HEMIPTERA** (Fig. 326–328).—True Bugs. Hemimetabolic; piercing and sucking mouth parts; wingless or with two pairs of wings, the fore wings thickened at the base. The labium forms a jointed beak into which the slender, piercing maxillæ and mandibles move. This order contains many families of interesting and economically important species, a few of which

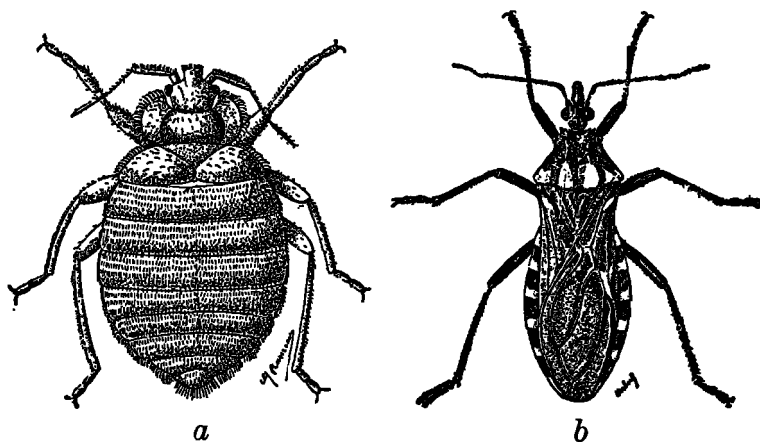


FIG. 327. — *a*, CIMICIDÆ. *Cimex lectularius*, the bed bug. *b*, REDUVIIDÆ. *Triatoma megista*, a kissing bug. (From Brumpt.)

are as follows. The water boatmen, CORIXIDÆ (Fig. 326, *a*), have long, flat, fringed metathoracic legs adapted for swimming; they carry a film of air about the body while under the water. The back swimmers, NOTONECTIDÆ, likewise have oar-like hind legs, but swim on their backs. The water scorpions, NEPIDÆ (Fig. 326, *b*), obtain air through a long caudal tube that is thrust through the surface; a common long, slender species is *Ranatra americana*. The giant water bugs, BELOSTOMATIDÆ (Fig. 326, *c*), are sometimes called electric-light bugs; their hind legs are also adapted for swimming; some tropical species reach a length of four or five inches; common species are *Lethocerus americanus*,

which has a femoral groove on each front leg into which the tibia fits, and *Belostoma flumineum* the female of which fastens her eggs on the back of the male. The water striders, GERRIDÆ (Fig. 326, d)

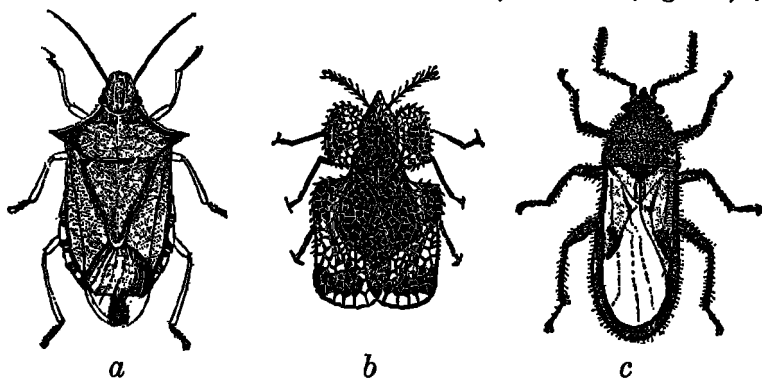


FIG. 328. — a, PENTATOMIDÆ. *Podisus spinosus*, a stink bug or soldier bug. b, TINGIDÆ. *Corythuca arcuata*, a lace bug. c, LYGAIDÆ. *Blissus leucopterus*, a chinch bug. (a, after Lugger; b, after Comstock; c, after Webster and Riley.)

have long, slender middle and hind legs which do not break through the surface film as they skim about over the water. The leaf bugs, NERIDÆ, are very numerous and often injurious to plants,



FIG. 329. — CICADIDÆ. Six stages in the emergence of an adult harvest fly, or cicada, from the nymph. (After Snodgrass.)

and include such common species as the tarnished plant bug, *Lygus pratensis*, and the apple red bug, *Lygidea mendax*. The bedbugs, CIMICIDÆ, are nocturnal insects that live on warm-blooded animals; the human species, *Cimex lectularius* (Fig. 327, a),

has been accused of transmitting various diseases but has not been definitely incriminated. The assassin bugs, *REDUVIINÆ*, form a large family that contains among others, certain species known as kissing bugs; several of these, especially *Triatoma megista* (Fig. 327, b), are responsible for the transmission of the PROTOZOA (trypanosomes) responsible for the human disease of South America known as Chagas disease. The lace bugs, *TINGIDÆ* (Fig. 328, b), have front wings, or hemelytra, of lace-like

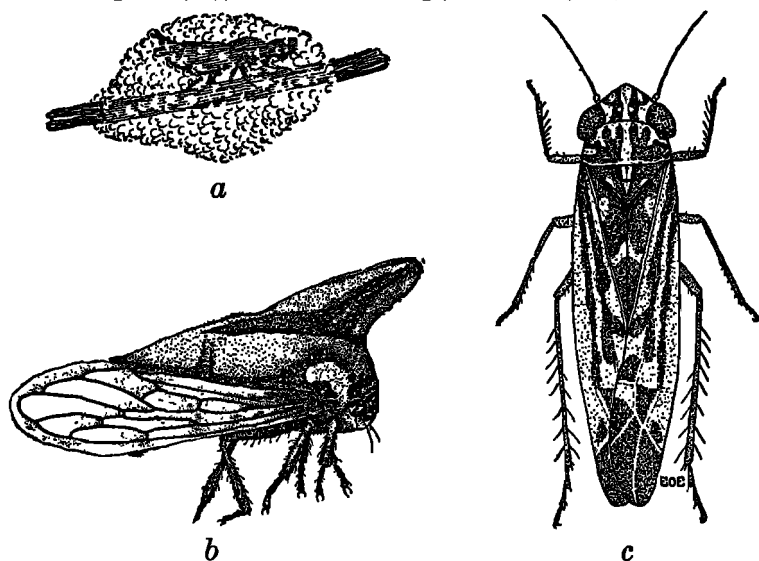


FIG. 330. — a, CERCOPIDÆ. *Aphrophora*, a spittle insect. b, MEMBRACIDÆ. *Platycotis vittata*, an oak tree hopper. c, CICADELLIDÆ. *Empoasca mali*, the apple leaf hopper. (a, after Morse; b, after Woodworth; c, from Essig.)

structure, as well as expansions of the prothorax and are hence easily recognized. The chinch bugs, *LYGÆIDÆ*, belong to a large family, the most notorious species being the common chinch bug, *Blissus leucopterus* (Fig. 328, c), that has been so destructive to grain, especially in the Mississippi Valley. The squash bug family, *COREIDÆ*, also contains many species, a good example of which is the common squash bug, *Anasa tristis*. The stink bugs, *PENTATOMIDÆ* (Fig. 328, a), secrete a fluid with a nauseous odor, hence their name; the cabbage bug, *Murgantia histrionica*, is destructive to garden vegetables, but another species, *Perillus bioculatus* is beneficial because it destroys potato beetles.

**Order 15. HOMOPTERA** (Figs. 329-332). — Cicadas, Leafhoppers, Aphids, Scales. Hemimetabolic; mouth parts for piercing and sucking; usually two pairs of wings of uniform thickness held over the back like the sides of a roof. Many economically important insects belong to this order. Several of the families are as follows. The cicadas, and harvest flies, *CICADIDÆ* (Fig. 329), are large, noisy insects; the best-known species is the periodical cicada, or seventeen-year locust, *Magicicada septendecim*, the nymphal stages of which live in the ground for seventeen years before the imago emerges. The spittle insects, or frog hoppers, *CERCOPIDÆ* (Fig. 330, *a*), live in a mass of froth elaborated from matter voided from the anus and mixed with a glue-like secretion from abdominal glands. The tree hoppers, *MEMBRACIDÆ* (Fig. 330, *b*), have a prothorax that extends back over the body and sometimes forms horn-like projections, as in the buffalo tree

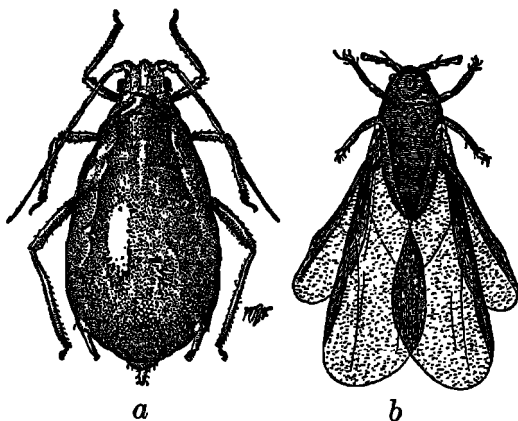


FIG. 331. — *a*, *APHIDIDÆ*. *Rhopalosiphum prunifoliae*, the apple-grain aphid, wingless form. *b*, *PHYLLOXERIDÆ*. *Phylloxera vitifoliae*, the grape phylloxera. (*a*, from Wellhouse; *b*, from Sedgwick.)

hopper, *Ceresa bubalus*, or a hump-back, as in *Telamona ampelopsidis*. The leaf hoppers, *CICADELLIDÆ* (Fig. 330, *c*), are small and abundant on grass; some are destructive, such as *Euscelis exitiosus*, on grain, *Erythroneura comes* on grape leaves and *Empoasca fabae*, on potatoes. The plant lice or aphids, *APHIDIDÆ* (Fig. 331, *a*), are mostly small, green insects with or without wings, that suck juices from plants; they secrete from the anus a sweet substance, known as honeydew, which is attractive to ants, bees, and wasps, sometimes bringing about a sort of symbiotic relationship between the aphids and other insects. The life cycle of aphids is of great interest. Stem mothers that are parthenogenetic and viviparous hatch from eggs that have lived through

the winter. Their offspring are wingless, parthenogenetic females. These give rise to wingless parthenogenetic females, but after a time produce winged females which migrate to other plants. As fall approaches, males and viviparous females appear, mating occurs, and fertilized eggs are laid that remain dormant over winter and give rise to stem mothers in the spring. Among the aphids are the green bug, *Toxoptera graminum*, a pest on wheat

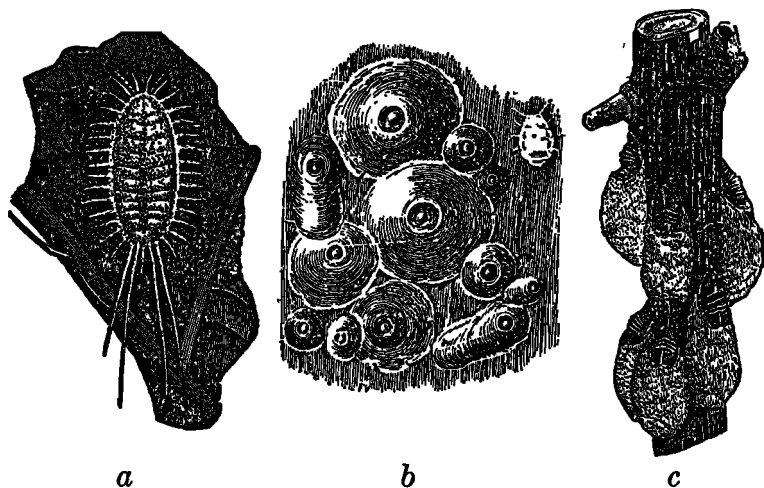


FIG. 332. — COCCIDÆ. a, *Pseudococcus longispinus*, the long-tailed mealy bug. b, *Aspidiotus perniciosus*, the San José scale. c, *Pulvinaria vitis*, the cottony maple scale, females with egg sacs. (After Comstock.)

and oats, the corn-root aphid, *Anuraphis maidiradicis*, the woolly apple aphid, *Eriosoma lanigera*, and a number of species that produce plant galls, such as the witch-hazel cone gall aphid, *Homaphis hamamelidis*. The phylloxerids, PHYLLOXERIDÆ, are also destructive to vegetation, especially the grape phylloxera, *Phylloxera vitifoliae* (Fig. 331, b). The white flies, ALEYRODIDÆ, are covered with a whitish powder, hence their name; the greenhouse white fly, *Asterochilton vaporariorum*, is an important pest. The scale insects and mealy bugs, COCCIDÆ (Fig. 332), are the most serious pests of horticulturists; they include the San José scale, *Aspidiotus perniciosus* (Fig. 332, b), the cottony maple scale, *Pulvinaria vitis* (c), the cottony cushion scale, *Icerya purchasi*, and the mealy bug, *Pseudococcus longispinus* (a); several species are useful to man, such as the lac insect, *Tachardia lacca*,

the cochineal insect, *Coccus cacti*, and the China wax insect, *Eri-cerus pe-la*.

**Order 16. DERMAPTERA** (Fig. 333). — Earwigs. Hemimetabolic; chewing mouth parts; wingless or with one or two pairs of wings, the fore wings small, leathery, and meeting in a straight line along the back, the hind wings, large, membranous, and folded lengthwise and crosswise under the fore wings; forceps-like cerci at posterior end of abdomen. The earwigs are nocturnal

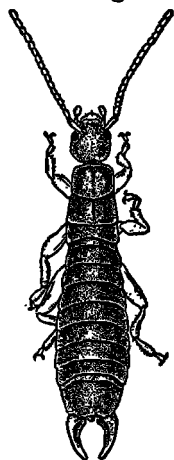


FIG. 333. — DERMAPTERA. *Anisolabis maritima*, the seaside earwig. (From Davenport.)

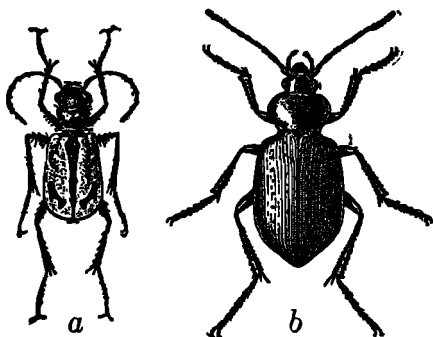


FIG. 334. — a, CICINDELIDÆ. A tiger beetle. b, CARABIDÆ. A ground beetle. (After Bruner and Howard.)

insects that feed principally on vegetation. The European earwig, *Forficula auricularia*, has been introduced into this country; the seaside earwig, *Anisolabis maritima* (Fig. 333), occurs along the Atlantic coast; the little earwig, *Labia minor*, is a widespread native species.

**Order 17. COLEOPTERA** (Figs. 334-340). — Beetles. Holometabolic; chewing mouth parts; wingless or with two pairs of wings, the fore wings being hard and sheath-like (elytra) and the hind wings being membranous and folded under the elytra; the prothorax large and movable. The COLEOPTERA are so numerous and separated into so many families that they are difficult to discuss in a short space. The plan adopted here is to list some of the more important groups and point out their more interesting and important characteristics.

**Suborder 1. ADEPHAGA.** — Carnivorous Beetles.

Family CICINDELIDÆ (Fig. 334, a). — Tiger beetles. Predacious; diurnal; usually metallic green or bronze,

banded or spotted with yellow; legs adapted for running; larvæ in vertical burrows in ground. Ex. *Cicindela dorsalis*, *C. punctulata*, *Tetracha carolina*.

Family CARABIDÆ (Fig. 334, b). — Ground beetles. Predacious, nocturnal; usually black and shiny; legs adapted for running. Ex. *Calosoma scrutator*, *Pæcilus lucublandus*, *Harpalus caliginosus*.

Family DYTISCIDÆ. — Predacious diving beetles. Aquatic; antennæ thread-like; hind legs adapted for swimming;

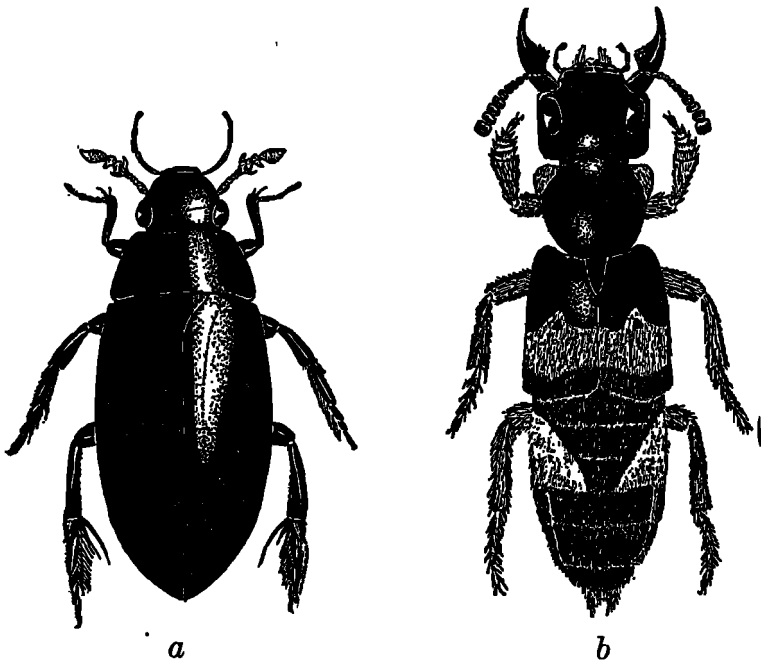


FIG. 335. — a, HYDROPHILIDÆ. *Hydrous triangularis*, the giant water-scavenger beetle. b, STAPHYLINIDÆ. *Creophilus mazillosus*, the hairy rove beetle. (From Essig.)

tarsi of fore legs of some species with suckers; air held under elytra while under water; larvæ are "water tigers." Ex. *Dytiscus fasciventris*, *Colymbetes sculptilis*, *Cybister fimbriolatus*.

Family GYRINIDÆ. — Whirligig beetles. Aquatic; social in habit; eyes divided into lower and upper halves; middle



and hind legs adapted for swimming; secrete ill-smelling whitish liquid. Ex. *Dineutus vittatus*, *Gyrinus borealis*.

**Suborder 2. POLYPHAGA.** — Herbivorous Beetles.

Family HYDROPHILIDÆ. — Water scavenger beetles. Aquatic; antennæ club-shaped; carry film of air underneath the body. Ex. *Hydrophilus obtusatus*, *Hydrous triangularis* (Fig. 335, a).

Family SILPHIDÆ. — Carrion beetles. Antennæ club-shaped; legs adapted for running; feed mostly on decaying animals. Ex. *Necrophorus marginatus* (burying beetle), *Silpha noveboracensis*.

Family STAPHYLINIDÆ. — Rove beetles. Small, slender; elytra short; abdominal segments movable; legs adapted

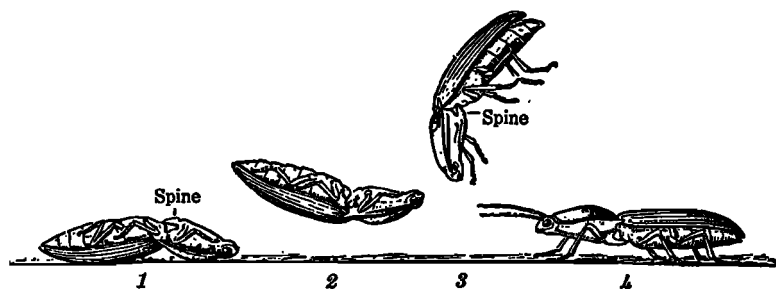


FIG. 336. — ELATERIDÆ. A click beetle turning over in the air to its normal position. (From Schmeil.)

for running. Ex. *Staphylinus maculosus*, *Creophilus maxillosus* (Fig. 335, b).

Family LAMPYRIDÆ. — Fireflies. Antennæ saw-like; prothorax expanded over head; nocturnal; emit light; larvæ and wingless females are "glow worms." Ex. *Photinus scintillans*, *Photuris pennsylvanica*.

Family MELOIDÆ. — Blister beetles and oil beetles. When dried and pulverized produce blister on skin; European species called "Spanish fly"; undergo hypermetamorphosis. Ex. *Epicauta vittata*, *Meloe angusticollis*.

Family ELATERIDÆ (Fig. 336). — Click beetles. Antennæ serrate; body flattened; larvæ are wireworms; leaps (clicks) by means of action of prosternal process in metasternal groove. Ex. *Alaus oculatus*, *Elater nigricollis*.

Family BUPRESTIDÆ (Fig. 337, *a*). — Metallic wood borers. Antennæ serrate; body hard, inflexible, flattened; bronze or metallic in color; larvæ mostly "flat-headed" borers. Ex. *Chalcophora virginica*, *Chrysobothris femorata*, *Agilus ruficollis* (causes raspberry gouty gall).

Family DERMESTIDÆ. — Dermestids. Small; elytra cover abdomen; adults feign death; feed on furs, wool, household goods. Ex. *Dermestes lardarius* (larder beetle), *Anthrenus scrophulariæ* (carpet beetle, Fig. 337, *b*), *Anthrenus museorum* (museum pest).

Family TENEBRIONIDÆ. — Darkling beetles. Black; fore and middle tarsi with five segments, hind tarsi with four

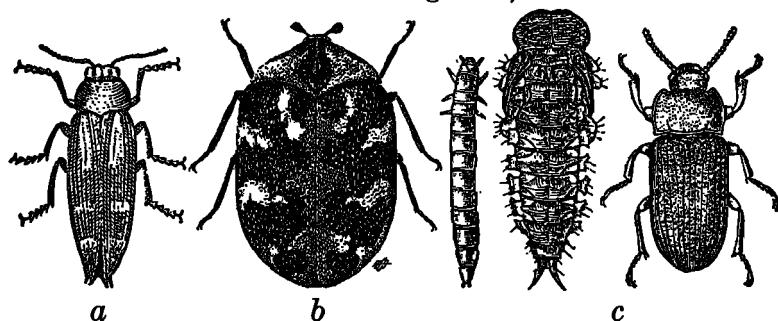


FIG. 337. — *a*, BUPRESTIDÆ. A metallic wood borer. *b*, DERMESTIDÆ. *Anthrenus scrophulariæ*, the "buffalo bug" or "buffalo moth." *c*, TENEBRIONIDÆ. *Tenebrio molitor*, the meal worm; larva, pupa and adult. (From various authors.)

segments; food, dry vegetable matter. Ex. *Tenebrio molitor* (meal worm, Fig. 337, *c*), *Bolitotherus cornutus* (fungus beetle).

Family COCCINELLIDÆ. — Ladybird beetle. Mostly predacious; some feed on scale insects; hemispherical in shape; red, yellow, or black with black, white, red, or yellow spots. Ex. *Rodolia cardinalis*, *Adalia bipunctata* (Fig. 338, *a*).

Family SCARABÆIDÆ. — Scarabæids or lamellicorn beetles. Club of antennæ lamellate. Ex. *Ateuchus sacer* (Egyptian scarab, Fig. 338, *b*), *Canthon lævis* (tumble bug), *Phyllophaga fusca* (June bug), *Macrodactylus subspinosus* (rose bug), *Dynastes tityrus* (rhinoceros beetle), *Euphoria inda* (bumble flower beetle).

Family LUCANIDÆ. — Stag beetles. Large, sometimes branched, mandibles; club of antennæ of flattened plates. Ex. *Lucanus dama*, *Dorcus parallelus*.

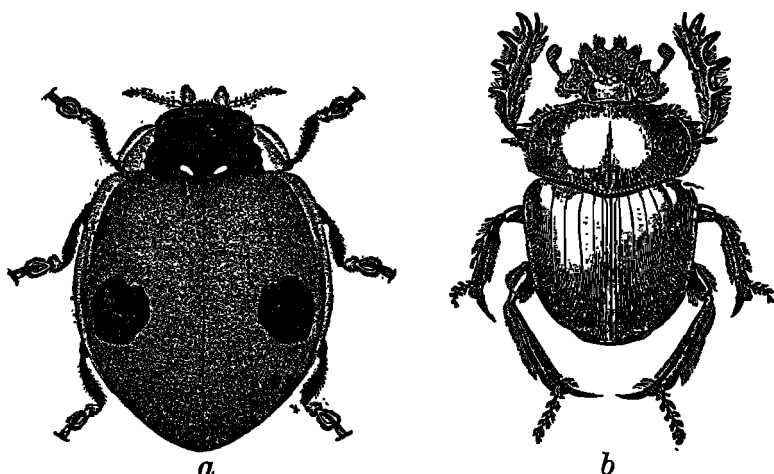


FIG. 338. — a, COCCINELLIDÆ. *Adalia bipunctata*, the two-spotted ladybird beetle. b, SCARABÆIDÆ. *Ateuchus sacer*, the sacred beetle of the Egyptians. (a, from Essig; b, from Sharp.)

Family PASSALIDÆ. — One species, *Passalus cornutus*, common in the United States.

Family CERAMBYCIDÆ (Fig. 339, a). — Long-horned beetles. Antennæ often longer than body, of eleven segments; tarsi with four segments, third bilobed, fourth very

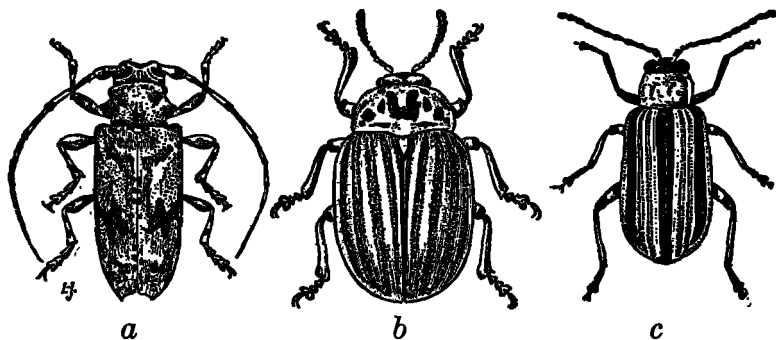


FIG. 339. — a, CERAMBYCIDÆ. *Acanthoderes decipiens*, a long-horned beetle. b, CHRYSOMELIDÆ. — *Leptinotarsa decemlineata*, the potato beetle. c, CHRYSOMELIDÆ. *Diabrotica vittata*, the striped cucumber beetle. (After various authors.)

small; larvæ, boring grubs. Ex. *Prionus laticollis*, *Cyllene robinix* (locust borer), *Tetraopes tetraophthalmus* (milkweed beetle).

Family CHRYSOMELIDÆ (Fig. 339, b, c). — Leaf beetles. Body, oval; antennæ and legs short; feed on leaves. Ex. *Lep tinotarsa decemlineata* (potato beetle, Fig. 339, b), *Haltica chalybea* (flea beetle), *Cassida nigripes* (tortoise beetle).

Family CURCULIONIDÆ. — Snout beetles. Head prolonged into snout. Ex. *Anthonomus grandis* (cotton-boll weevil, Fig. 340, a), *Balaninus rectus* (acorn weevil).

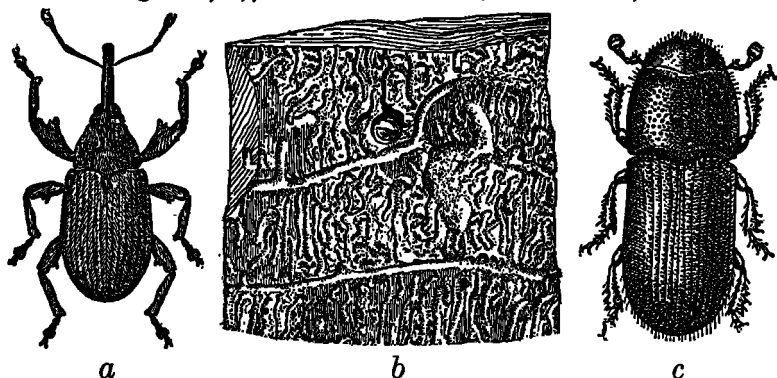


FIG. 340. — a, CURCULIONIDÆ. *Anthonomus grandis*, the cotton-boll weevil. b, SCOLYTIDÆ. Galleries of an engraver beetle under the bark of a tree. c, SCOLYTIDÆ. *Dendroctonus frontalis*, the southern pine beetle. (After Felt and Hopkins.)

Family SCOLYTIDÆ (Fig. 340, b, c). — Engraver and ambrosia beetles. Some live on fungus (ambrosia); others are called timber beetles. Ex. *Scolytus rugulosus* (fruit tree bark beetle), *Dendroctonus punctatus* (spruce beetle).

Order 18. STREPSIPTERA (Fig. 341, a). — Stylopids. Hypermetamorphosis; mouth parts vestigial or absent; endoparasitic in other insects; male with club-shaped fore wings and large membranous hind wings; female, wingless and legless; nutrition by absorption; life cycle complex. The stylopids live principally in bees, wasps, and homopterous bugs. Ex. *Xenos wheeleri* a parasite of the wasp, *Polistes metricus*.

Order 19. MECOPTERA (Fig. 341, b). — Scorpion flies. Holometabolic; chewing mouth parts; antennæ long and slender; head

prolonged into beak; wingless or with two pairs of long, narrow, membranous wings; males with clasp ing organ at caudal end resembling the sting of a scorpion; food, fruit, and dead insects. Ex. *Panorpa rufescens*, *Bittacus strigosus*.

**Order 20. TRICHOPTERA** (Fig. 342). — Caddice flies. Holometabolic; vestigial mouth parts in adult; two pairs of membranous

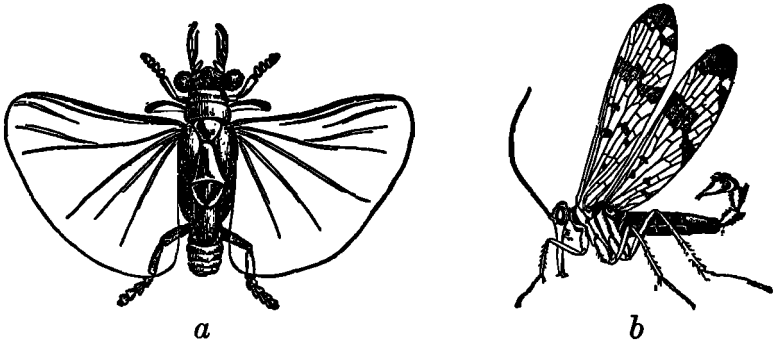


FIG. 341. — a, STREPSIPTERA. A twisted-winged insect. b, MECOPTERA. *Panorpa*, a scorpion fly. (a, after Packard; b, after Sharp.)

wings clothed with long, silky hairs; the aquatic larvæ build portable cases of sand grains or vegetable matter fastened together with silk secreted by modified salivary glands. Members

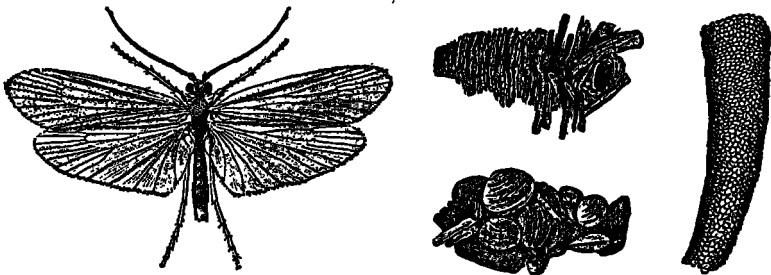


FIG. 342. — TRICHOPTERA. An adult caddice fly, with wings spread, and three types of larval cases. (After several authors.)

of the genus *Hydropsyche* construct non-portable nets in moving water. Ex. *Phryganea interrupta* (case of pieces of leaves), *Molanna cinerea* (case of sand).

**Order 21. LEPIDOPTERA** (Figs. 343–346). — Butterflies, skippers, and moths. Holometabolic; sucking mouth parts; wingless or

with two pairs of membranous wings covered with overlapping scales. The sucking apparatus, which is coiled underneath the head, consists of the two half-round maxillæ fastened together so as to form a tube. The larvæ are called caterpillars. They sometimes spin a cocoon in which they pupate. The pupa is often called a chrysalis. It is customary to divide the LEPIDOPTERA into two groups, the moths (HETEROCERA) and butterflies (RHOPALOCERA). One family of butterflies, the HESPERIIDÆ, are often set apart and called skippers. Moths are mostly nocturnal and their antennæ are usually thread-like or feather-like and without a terminal knob. Butterflies are diurnal; the antennæ are thread-like and have a knob at the end; and the wings are held vertically over the back when at rest. Skippers are diurnal; the antennæ are thread-like and have a subterminal knob and a terminal recurved hook; and they have a skipping mode of flight. Space allows listing of only a few families.

Family INCURVARIIDÆ. — Ex. *Yucca* moth, *Tegeticula alba*.

The flowers of the genus *Yucca* depend upon this species



FIG. 343. — a, TINEIDÆ. *Tinea pellionella*, a clothes moth. b, NOCTUIDÆ. *Heliothis obsoleta*, the cotton-boll worm or corn earworm. (From Herrick.)

for their cross-pollination. The moth visits the flowers in the evening; scrapes some pollen from a stamen, holds it underneath its head, and carries it to another flower. It clings to the pistil of this, and, thrusting its ovipositor through the wall of the ovary, lays an egg. It then mounts the pistil, and forces the pollen it has brought, down into the stigmatic tube. Another egg is laid in another part of the ovary, and more pollen is inserted into the stigmatic tube. These processes may be repeated half a dozen times in a single flower. The advantage to the flower is, of course, the certainty of being cross-pollinated and of producing seeds. These seeds provide a supply of food for the larvæ that hatch

from the eggs laid by the moth in the ovary. The seeds are so numerous that the few eaten by the larvæ may well be spared.

Family TINEIDÆ. — Clothes moths. Ex. *Tinea pellionella* (Fig. 343, a).

Family GELECHIIDÆ. — Ex. Angoumois grain moth, *Sitotroga cerealella*; Pink boll worm, *Pectinophora gossypiella*.



FIG. 344. — SPHINGIDÆ. A hawk moth. a, adult; b, larva; c, pupa. (From U. S. Dept. Agric.)

Family TORTRICIDÆ. — Ex. Codling moth, *Carpocapsa pomonella*.

Family PYRALIDIDÆ. — Ex. European corn borer, *Pyrausta nubilalis*; bee moth, *Galleria mellonella*; Mediterranean flour moth, *Ephestia kuhniella*.

Family SPHINGIDÆ (Fig. 344). — Hawk moths. Ex. White-lined sphinx, *Celerio lineata*; tomato worm, *Protoparce quinquemaculata*.

Family GEOMETRIDÆ. — Measuring worms. Ex. Fall canker worm, *Alsophila pometaria*.

Family LYMANTRIIDÆ. — Tussock moths. Ex. White-marked tussock moth, *Hemerocampa leucostigma*; gypsy moth,

*Porthetria dispar*; brown-tail moth, *Euproctis chrysorrhæa*.

Family NOCTUIDÆ. — Owlet moths. Ex. Cotton worm, *Alabama argillacea*; army worm, *Cirphis unipuncta*; cotton-boll worm, *Heliothis obsoleta* (Fig. 343, b).

Family ARCTIDÆ. — Tiger moths. Ex. Fall webworm, *Hyphantria cunea*; yellow bear, *Diacrisia virginica* (hairy caterpillars).

Family CITHERONIDÆ. — Ex. Regal moth, *Citheronia regalis* (larva in the hickory horned devil); Imperial moth, *Basilona imperialis*.

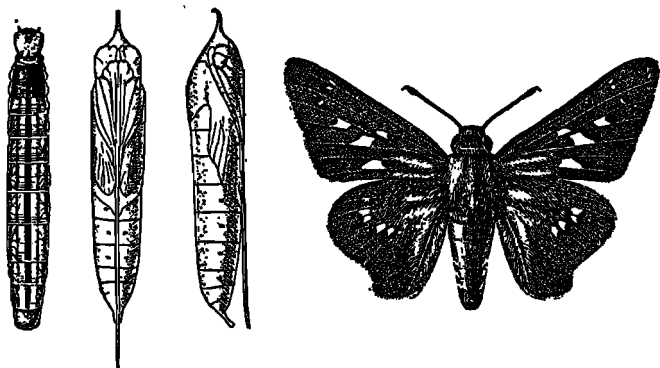


FIG. 345. — HESPERIDÆ. *Calpodus ethlius*, a skipper; adult, pupæ and larva. (After Chittenden.)

Family SATURNIDÆ. — Giant silkworm moths. Ex. Polyphemus, *Telea polyphemus*; luna, *Tropæa luna*; promethea, *Callosamia promethea*; cecropia, *Samia cecropia*.

Family BOMBYCIDÆ. — Silkworm moths. Ex. Silkworm, *Bombyx mori*.

Family HESPERIDÆ (Fig. 345). — Skippers. Silver-spotted skipper, *Epargyreus tityrus*; cloudy wing, *Thorybes pylades*.

Family PAPILIONIDÆ. — Swallow-tailed butterflies. Ex. Tiger swallow-tail, *Papilio glaucus*. The adults occur in two forms, *Papilio glaucus turnus* and *Papilio glaucus glaucus*. *Papilio polyxenes* is known as the black swallow-tail (Fig. 346).

Family PIERIDÆ. — Ex. Cabbage butterfly, *Pieris rapæ*; clouded sulphur, *Eurymus philodice*.



Family NYMPHALIDÆ. — Ex. Spangled fritillary, *Argynnis cybele*; mourning cloak, *Ewanessa antiopa*; viceroy, *Basilarchia archippus* (mimics the monarch); monarch, *Danaus archippus*.

Family LYCÆNIDÆ. — Gossamer-winged butterflies. Ex. Banded hair streak, *Thecla calanus*; American copper,

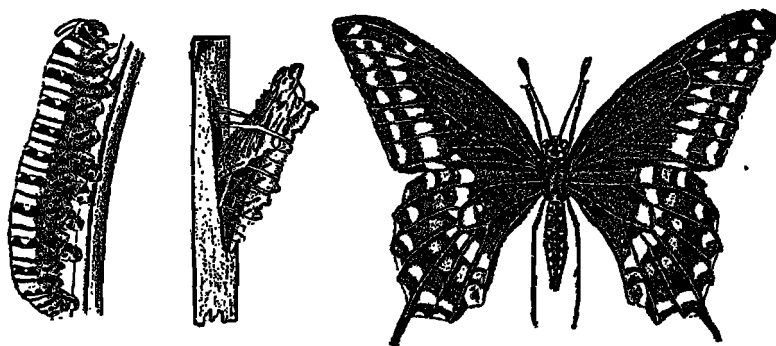


FIG. 346. — PAPILIONIDÆ. *Papilio polyzenes*, the black swallow-tail, larva, pupa and adult. (After Webster.)

*Heodes hypophlæas*; spring azure, *Lycæna argiolus* (very polymorphic, over a dozen forms named from North America).

**Order 22. DIPTERA** (Figs. 347-354). — Flies. Holometabolic; piercing and sucking mouth parts forming a proboscis; wingless or with one pair of membranous fore wings, the hind wings being represented by knobbed threads called halteres; larvæ known as maggots; larval skin sometimes serves as a cocoon and called a puparium. The labium usually serves as a guide for the slender, piercing mandibles and maxillæ, and for the sucking tube, consisting of an elongated epipharynx from the roof of the mouth and an elongated hypopharynx from the floor of the mouth, which is thrust into the wound and through which juices are sucked up by means of a pharyngeal pump in the head. Many variations exist in the mouth parts of DIPTERA.

**Suborder 1. ORTHORRHAPHA.** — Larva with well-chitinized head capsule; pupa enclosed in pupal skin; adult escapes from pupa by longitudinal slit in thoracic region.

**SECTION A. NEMOCERA.** — Flies with antennæ of more than five segments and usually long and slender.

Family TIPULIDÆ (Fig. 347, a). — Crane flies. Slender body; narrow wings; long legs; transverse V-shaped suture on dorsal surface of mesothorax. Ex. *Tipula abdominalis*; *Bittacomorpha clavipes*.

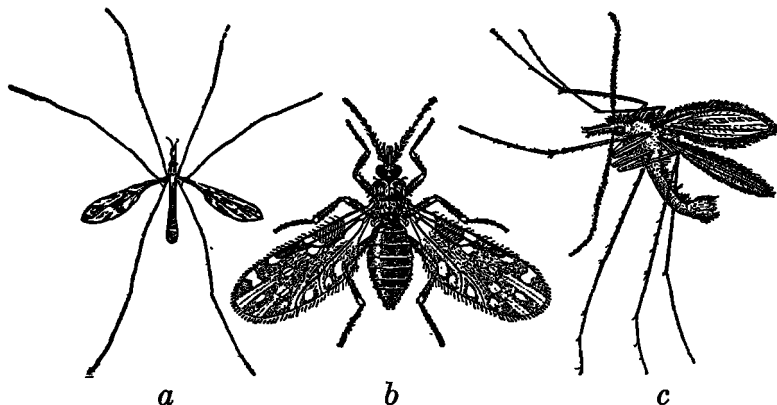


FIG. 347. — a, TIPULIDÆ. *Tipula*, a crane fly. b, CHIRONOMIDÆ. *Culicoides guttipennis*, a punkie or "no-see-um." c, PSYCHODIDÆ. *Phlebotomus papatasi*, a sand fly. (a, after Weed; b, after Pratt; c, after Newstead.)

Family CHIRONOMIDÆ. — Midges. Ex. *Culicoides guttipennis*, a punkie or "no-see-um" (Fig. 347, b).

Family PSYCHODIDÆ. — Moth flies. Ex. *Psychoda alternata*. Sand flies of the genus *Phlebotomus papatasi* (Fig. 347, c)

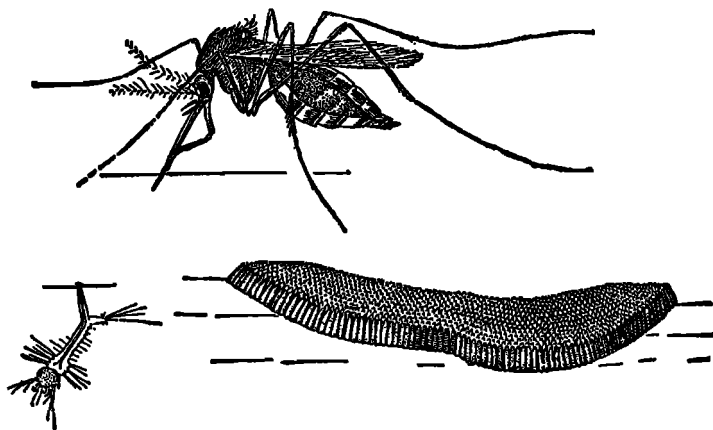


FIG. 348. — CULICIDÆ. *Culex pipiens*. Adult female, egg mass on surface of water, and young hanging from surface of water. (From Howard.)

transmit pappataci fever, oriental sore, and oroya fever from man to man.

Family CULICIDÆ. — Mosquitoes. Ex. *Culex pipiens*, house mosquito (Fig. 348); *Anopheles quadrimaculatus* (transmits malaria, Fig. 349, a); *Aedes ægypti* (transmits yellow

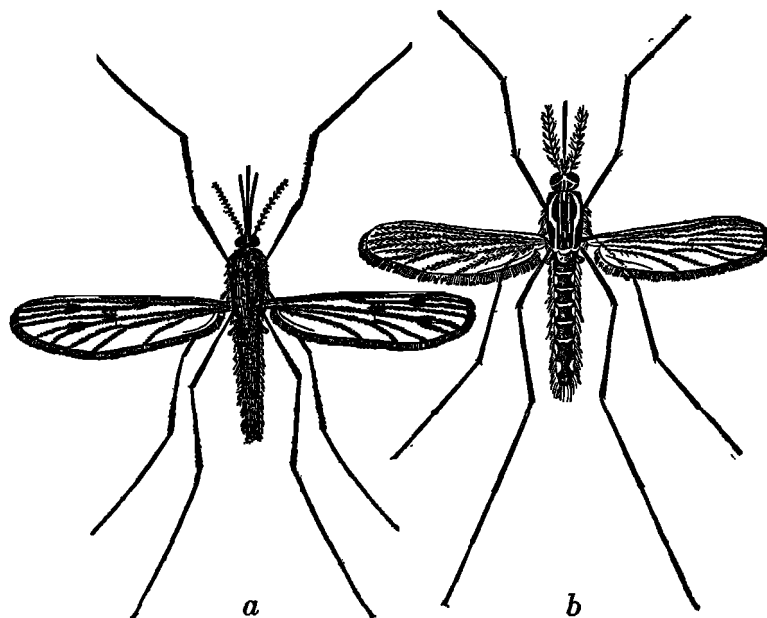


FIG. 349. — CULICIDÆ. a, *Anopheles quadrimaculatus*, a malaria mosquito. b, *Aedes ægypti*, the yellow fever mosquito. (After Herrick.)

fever, Fig. 349, b). Mosquitoes also transmit dengue and filariasis.

Family CECIDOMYIDÆ. — Gall gnats. Ex. *Rhabdophaga strobiloides* (causes willow-cone gall, Fig. 350); Hessian fly, *Phytophaga destructor*.

Family SIMULIIDÆ (Fig. 351, a). — Black flies. Ex. Adirondack black fly, *Prosimulium hirtipes*; buffalo gnat, *Eusimulium pecuarum*. These are blood-sucking pests of man and animals. *Simulium damnosum* transmits the human filarial worm; *Onchocerca volvulus* of Africa.

SECTION B. BRACHYCERA. — Flies with short, thick antennæ containing five or less segments.

Family TABANIDÆ. — Horseflies. Ex. *Tabanus atratus*; *Chrysops silacea* (transmits human filarial worm, *Loa loa*); *Chrysops discalis* (transmits tularæmia from jack rabbits to man, Fig. 351, b).

Family BOMBYLIIDÆ. — Bee flies. Ex. *Bombylius major* (Fig. 351, c). Adults resemble bees; larvæ feed on egg sacs of

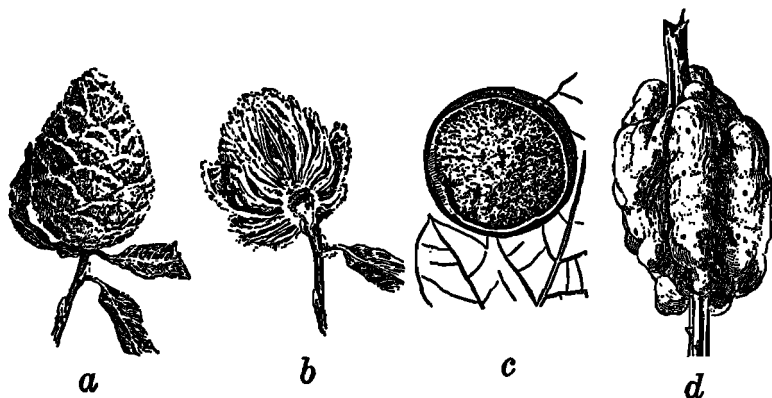


FIG. 350. — Plant galls due to the presence of insects. a, Willow-cone gall due to a fly of the family CECIDOMYIDÆ. b, Same cut open to show the maggots within. c, Oak-apple gall due to a hymenopterous insect, *Amphibolips confluens*, of the family CYNIPIDÆ. d, Blackberry-knot gall due to member of the family CYNIPIDÆ. (a, b, after Washburn; c, d, after Beutenmüller.)

ORTHOPTERA and on hymenopterous and lepidopterous larvæ.

Family ASILIDÆ (Fig. 351, d). — Robber flies. Ex. *Erax æstuanus*; *Asilus notatus*.

**Suborder 2. CYCLORRHAPHA.** — Pupa enclosed in last larval skin strengthened with chitin (puparium).

Family SYRPHIDÆ. — Flower flies. Ex. Drone fly, *Eristalis tenax* (larva known as rat-tailed maggot); *Syrphus perplexus*.

Family TRYPETIDÆ. — Ex. Mediterranean fruit fly, *Ceratitis capitata* (Fig. 352, a); goldenrod gall fly, *Eurosta solidaginis*.

Family PIOPHILIDÆ. — Ex. Cheese skipper, *Piophila casei* (Fig. 352, b, c).

Family EPHYDRIDÆ. — Ex. Petroleum fly, *Psilopa petrolei* (larva lives in crude petroleum).

FAMILY DROSOPHILIDÆ. — Pomace flies. Fruit fly, *Drosophila melanogaster* (Fig. 352, d, employed more extensively than any other animal for the study of genetics).

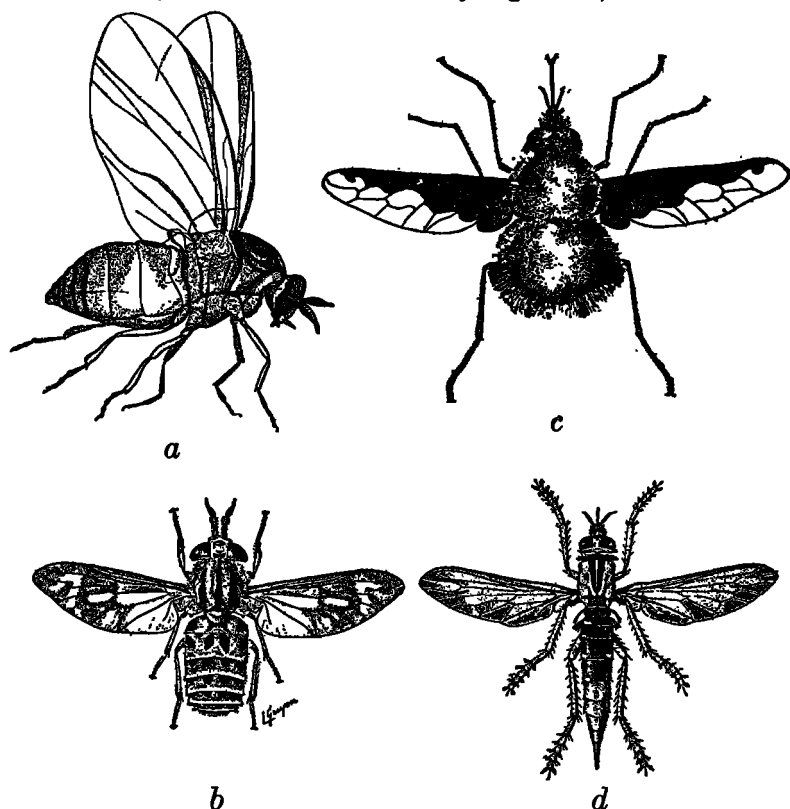


FIG. 351. — a, SIMULIIDÆ. *Simulium pictipes*, a black fly. b, TABANIDÆ. *Chrysops discalis*, the vector of tularæmia. c, BOMBYLIIDÆ. *Bombylius major*, a bee fly. d, ASILIDÆ. *Asilus crabroniformis*, a robber fly. (a, from Herrick; b, d, from Brumpt; c, from Essig.)

Family GASTEROPHILIDÆ. — Bot flies. Ex. Horse bot fly. *Gasterophilus intestinalis*.

Family ESTRIDÆ. — Bot and warble flies. Ex. Sheep bot fly, *Æstrus ovis*; heel fly, *Hypoderma lineatum*; *Dermatobia cyaniventris* (Fig. 352, e, may occur in skin of man).

Family CALLIPHORIDÆ. — Blow flies. Ex. Blow fly, *Calliphora vomitoria*; green-bottle fly, *Lucilia cæsar*; screw-worm fly,

*Chrysomya macellaria* (may infest nostrils of man). Stubborn cases of osteomyelitis have recently been treated successfully with the aid of blow-fly maggots.

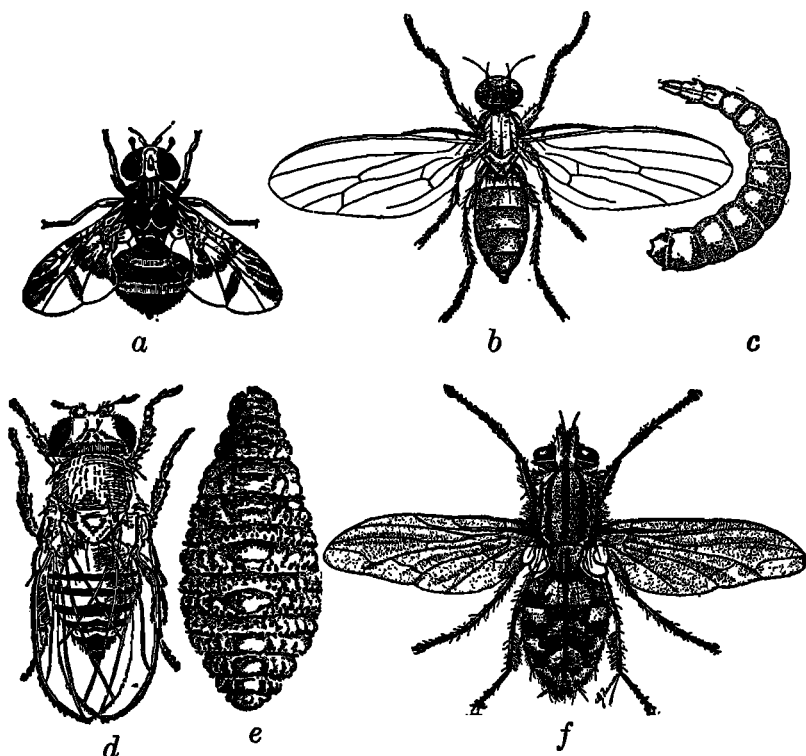


FIG. 352. — a, TRYPETIDÆ; *Ceratitis capitata*, the Mediterranean fruit fly. b, PIOPHILIDÆ; *Piophila casei*, the cheese skipper. c, Cheese skipper; the maggot of *P. casei*. d, DROSOPHILIDÆ; *Drosophila melanogaster*, a fruit fly. e, CESTRIDÆ; *Dermatobia cyaniventris*, larva of a bot fly. f, SARCOPHAGIDÆ; *Sarcophaga carnaria*, a flesh fly. (a, after Fuller; b, c, after Herrick; d, after Bridges; e, after Blanchard; f, after Brumpt.)

Family SARCOPHAGIDÆ (Fig. 352, f). — Ex. *Sarcophaga hæmorrhoidalis* (may cause intestinal myiasis in man); *Wohlfahrtia vigil* (may cause cutaneous myiasis in man). Several species live on dead insects in the cups of pitcher plants.

Family TACHINIDÆ. — Ex. *Trichopoda pennipes*. This and other species are important parasites of injurious insects.

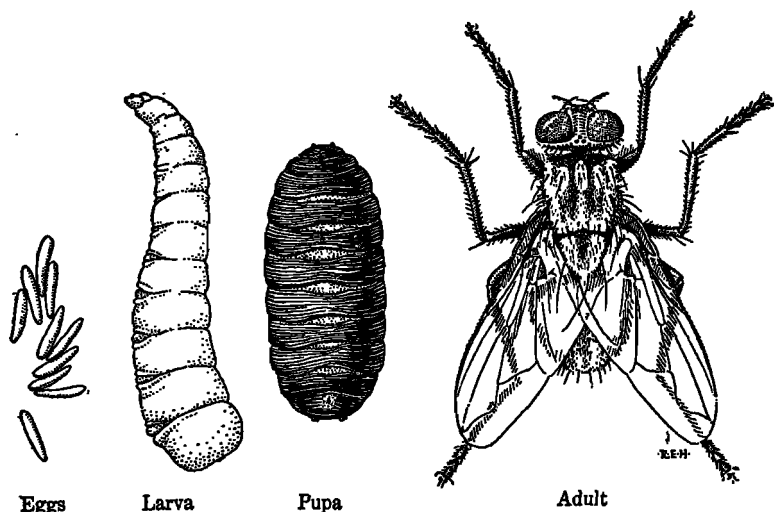


FIG. 353. — MUSCIDÆ. *Musca domestica*, the house fly. (From Woodruff.)

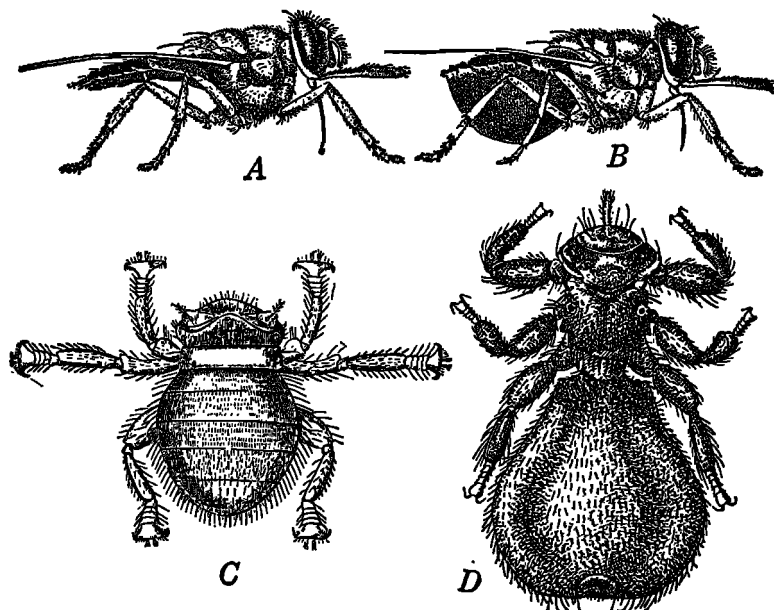


FIG. 354. — A, B, MUSCIDÆ; *Glossina palpalis*, the vector of African sleeping sickness, before (A) and after (B) a meal. C, BRAULIDÆ; *Braultia cæca*, a bee louse parasitic on the honeybee. D, HIPPOBOSCIDÆ; *Melophagus ovinus*, a sheep tick. (A, B, D, from Brumpt; C, after Meinert.)

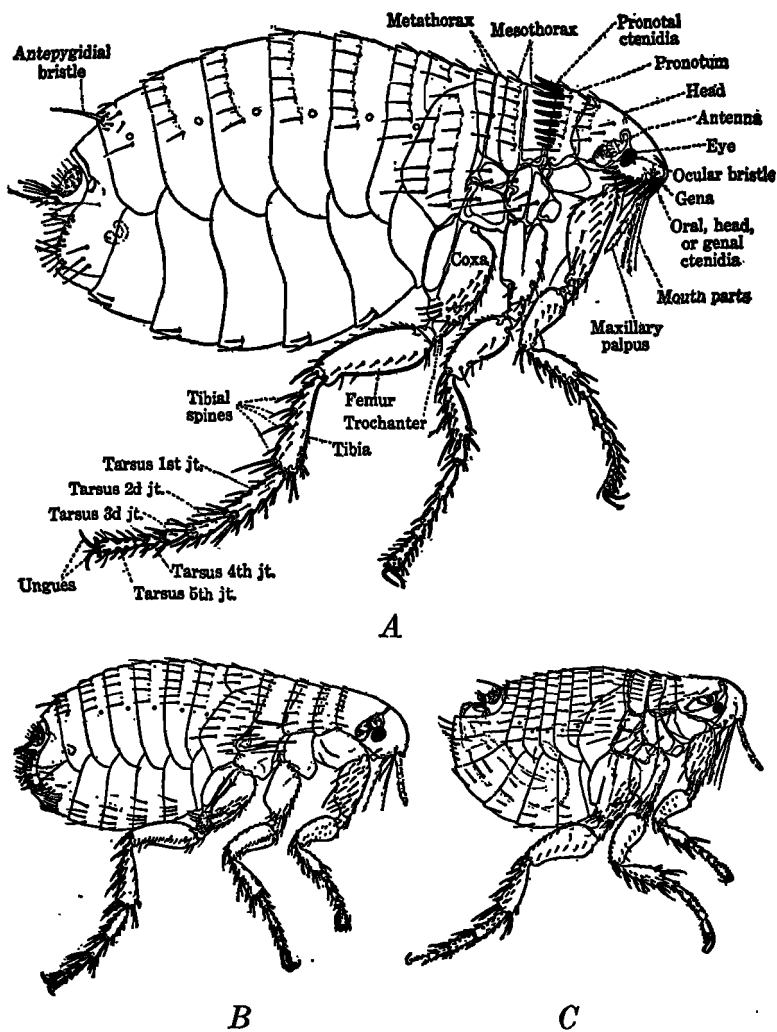


FIG. 355. — SIPHONAPTERA. Fleas. A, Diagram showing principal external features. B, *Pulex irritans*, the human flea, female. C, *Xenopsylla cheopis*, the oriental rat flea, male, the vector of bubonic plague. (From Herms.)



Family MUSCIDÆ. — Ex. House fly, *Musca domestica* (Fig. 353); stable fly, *Stomoxys calcitrans*; tsetse fly, *Glossina palpalis* (Fig. 354, A, B, transmit the protozoan parasite of sleeping sickness in Africa, see p. 47).

Family HIPPOBOSCIDÆ. — Louse flies. Ex. Sheep tick, *Melophagus ovinus* (Fig. 354, D).

Family BRAULIDÆ. — Bee lice. Ex. *Braula cæca*, a parasite of the honeybee (Fig. 354, C).

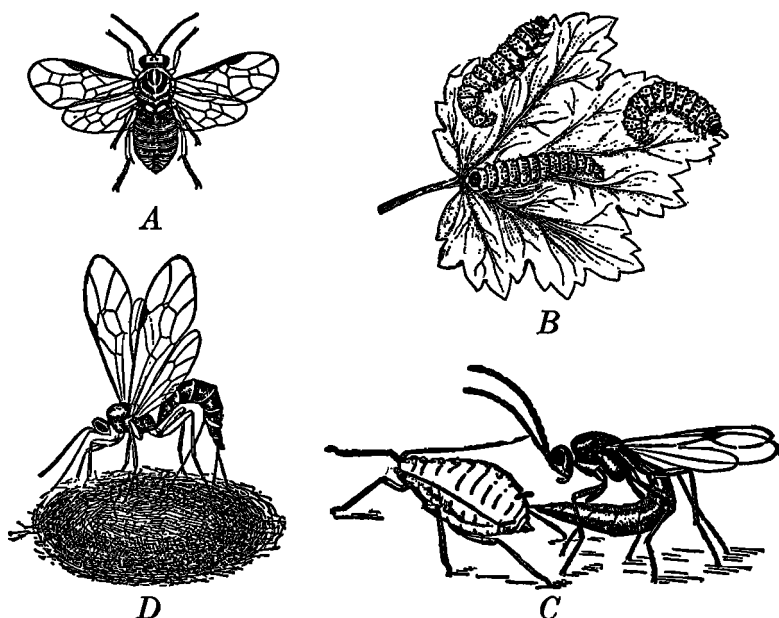


FIG. 356. — A, B, TENTHREDINIDÆ; *Pteronidea*. A, adult sawfly; B, larva, or currant worm. C, BRACONIDÆ; *Lysiphlebus*, a parasite on aphids. D, ICHNEUMONIDÆ; *Itopectis conquisitor*; female laying eggs in cocoon of tent caterpillar. (After various authors.)

Order 23. SIPHONAPTERA (Fig. 355). — Fleas. Holometabolic; piercing and sucking mouth parts; wingless; body laterally compressed; head small; no compound eyes; legs adapted for leaping; ectoparasites of mammals, a few of birds. Ex. Cat flea, *Ctenocephalus felis* (also attacks dog and man); dog flea, *C. canis* (also attacks cat and man); human flea, *Pulex irritans* (Fig. 355, B); rat flea, *Xenopsylla cheopis* (Fig. 355, C, transmits bubonic plague); sticktight flea, *Echidnophaga gallinacea* (serious pest of poultry);

chigoe or jigger, *Tunga penetrans*. (See also ACARINA, Family TROMBIDIIDÆ.)

**Order 24. HYMENOPTERA** (Figs. 356-364). — Holometabolic; chewing or sucking mouth parts; wingless or with two pairs of membranous wings, fore wings larger, venation reduced; wings on

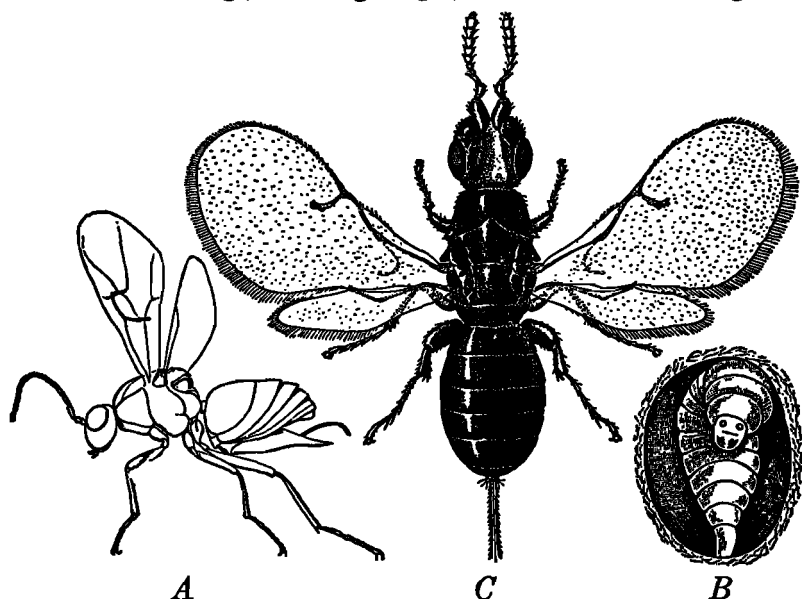


FIG. 357. — A, B, CYNIPIDÆ. A, *Rhodites rosæ*, causative agent of the mossy rose gall. B, larva of same in its cell. C, CHALCIDIDÆ. *Blastophaga psenes*, adult female fig insect. (A, B, after Sharp; C, from Essig.)

each side held together by hooks (hamuli); females usually with sting, piercer, or saw; some parasitic on other insects.

Family TENTHREDINIDÆ. — Sawflies. Ex. Currant worm, *Pteronidea ribesi* (Fig. 356, A, B); rose slug, *Cladius isomerus*.

Family BRACONIDÆ (Fig. 356, C). — Ex. *Microgaster facetosa* (parasitic on moths); *Aphidius rosæ* (parasitic on aphids).

Family ICHNEUMONIDÆ (Fig. 356, D). — Ichneumon flies. Ex. *Megarhyssa lunator* (parasitic on larva of pigeon horn-tail, *Tremex columba*); *Ophion bilineatum* (parasitic on skip-pers).

Family CYNIPIDÆ. — Gall flies and others. Ex. Oak hedgehog gall, *Andricus erinacei*; oak apple, *Amphibolips con-*

*fluens* (Fig. 350, c); mossy rose gall, *Rhodites rosæ* (Fig. 357, A, B).

Family CHALCIDIDÆ. — Ex. Chalcis fly, *Aphelinus jucundus* (parasitic on aphids); fig insect, *Blastophaga psenes* (Fig. 357, C, necessary for fertilization of fig tree flowers).

Family FORMICIDÆ. — Ants. Ants are all social insects and each colony contains several castes as in termites (p. 445). Ex. Red ant, *Monomorium pharaonis* (Fig. 358 B, a household nuisance); agricultural ant, *Pogonomyrmex*

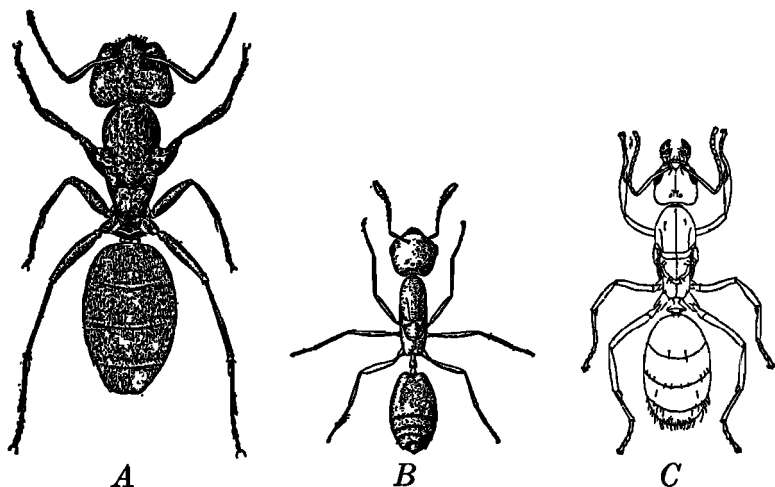


FIG. 358. — FORMICIDÆ. A, *Camponotus herculeanus* var. *pennsylvanicus*, the large black carpenter ant. B, *Monomorium pharaonis*, the red ant. C, *Iridomyrmex humilis*, the Argentine ant queen. (From Herrick.)

*barbatus*; shed builder, *Crematogaster lineolata* (builds sheds for aphids); fungus-growing ant, *Atta texana*; Argentine ant, *Iridomyrmex humilis* (Fig. 358, C, a household and orchard pest); carpenter ant, *Camponotus herculeanus* var. *pennsylvanicus* (Fig. 358, A); mound-building ant, *Formica exsectoides*; slave maker, *Formica sanguinea*; honey ant, *Myrmecocystus melliger* (certain individuals, repletes, serve as storage reservoirs).

Family VESPIDÆ. — Wasps. Ex. Solitary jug builder, *Eumenes fraternus*; social polistes, *Polistes pallipes*; white-faced hornet, *Vespa maculata* (Fig. 359, B); yellow jacket, *Vespa maculifrons* (Fig. 359, A).

Family SPHECIDÆ. — Digger wasps. Ex. Mud dauber, *Trypoxylon albitarsis*; tool-using wasp, *Sphex urnaria* (Fig. 360, A).

Family ANDRENIDÆ. — Ex. Mining bee, *Andrena vicina* (Fig. 360, B); carpenter bee, *Ceratina dupla*.

Family MEGACHILIDÆ. — Leaf-cutter bees. Ex. *Megachile brevis*.

Family BOMBIDÆ (Fig. 360, c). — Bumblebees. Nest-building bumblebee, *Bombus vagans*; usurper bumblebee, *Psithyrus laboriosus* (social parasite of other bumblebees).

Family APIDÆ. — Honeybees. One introduced species in the United States, *Apis mellifica* (Fig. 361). The mouth parts, legs, and sting of the worker honeybee are so

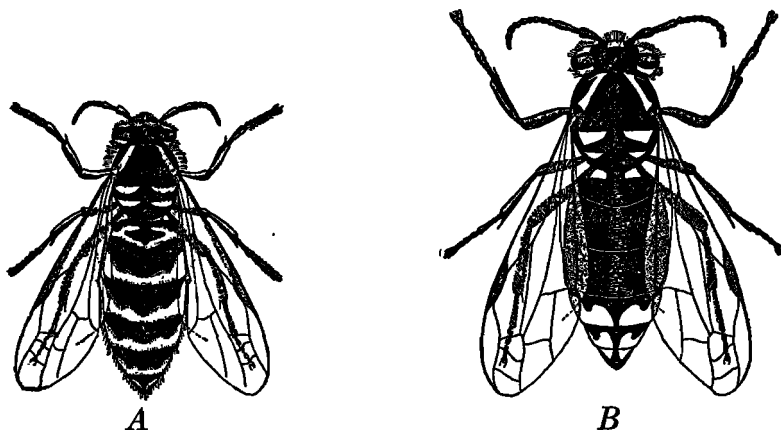
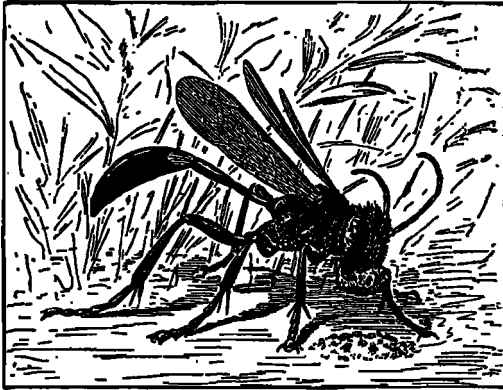


FIG. 359. — VESPIDÆ. A, *Vespa maculifrons*, the yellow jacket. B, *Vespa maculata*, the bald-faced hornet. (From Herrick.)

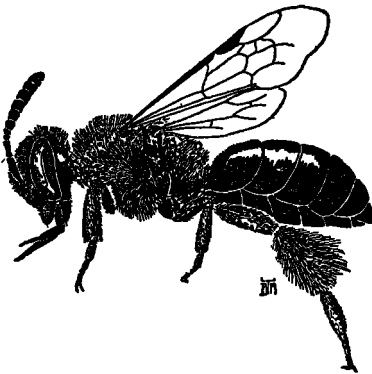
marvelously adapted for various functions that a description of them is presented here and the student is advised to study these structures in detail.

**Mouth parts** (Fig. 362). — The mouth parts consist of a labrum, or upper lip, the epipharynx, a pair of mandibles, two maxillæ, and a labium, or under lip. The *labrum* is joined to the *clypeus*, which lies just above it. From beneath the labrum projects the fleshy *epipharynx*; this is probably an organ of taste. The *mandibles*, or jaws, are situated one on either side of the labrum; they are notched in the queen and drone, but smooth in the worker. The

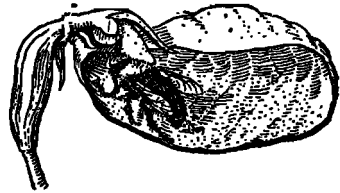
latter makes use of them in building honey-comb. The *labium* is a complicated median structure extending downward from beneath the labrum. It is joined to the back of the head by a triangular



A



B



C

FIG. 360. — A, SPHECIDÆ. *Spheg urnaria*; a digger wasp using a stone to pack earth over its nest. B, ANDRENIDÆ. *Andrena*, a mining bee. C, BOMBIDÆ. *Bombus*, a bumblebee pollinating a flower of the orchid *Cypripedium*. (After various authors.)

piece, the *submentum*. Next to this is a chitinous, muscle-filled piece, the *mentum*, beyond which is the *ligula*, or tongue, with one *labial palpus* on each side. The *ligula* may be drawn in or extended. It is long and flexible, with a spoon or *bouton* at the end. Hairs of various kinds are arranged upon it in regular rows; these are used

for gathering nectar, and as organs of touch and taste. The *maxillæ*, or lower jaws, fit over the mentum on either side. Along

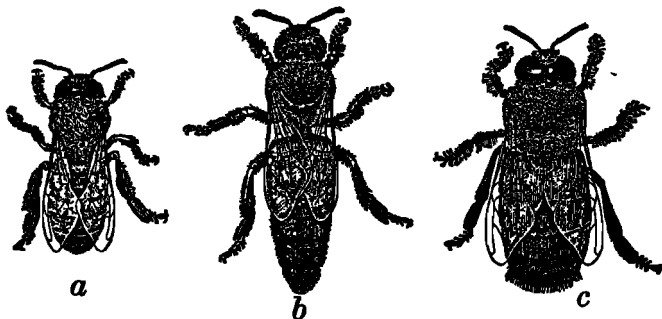


FIG. 361.—Honeybees. a, worker; b, queen; c, drone. (From Phillips.)

their front edges are rows of stiff hairs. *Maxillary palpi* are also present.

Nectar is collected in the following manner. The maxillæ and the labial palpi form a tube, in the center of which the tongue moves backward and forward. When the epipharynx is lowered, a passage is completed into the œsophagus. The nectar is first collected by the hairs on the ligula; it is then forced upward by the pressing together of the maxillæ and labial palpi.

*Legs* (Fig. 363).—The *prothoracic legs* possess the following useful structures. The femur and the tibia are clothed with *branched hairs* for gathering pollen. Extending on one side from the distal end of the tibia are a number of curved bristles, the *pollen brush*, which are used to brush up the pollen loosened by the coarser spines; on the other side is a flattened movable spine, the *velum*, which fits over a curved indentation in the first tarsal joint or metatarsus. This entire

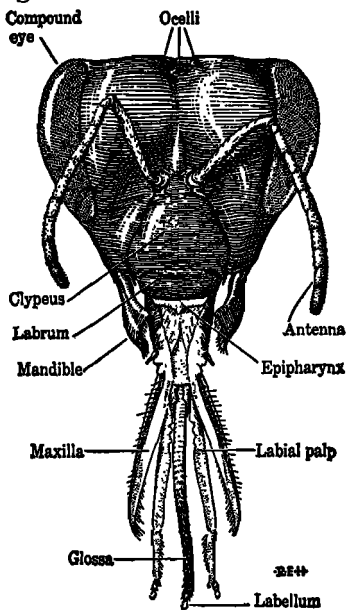


FIG. 362.—Head of honeybee. (From Woodruff.)

entire

structure is called the *antenna cleaner* and the row of teeth which lines the indentation is known as the *antenna comb*. On the front of the metatarsus is a row of spines called the *eye brush*, which is used to brush out any pollen or foreign particles lodged among the hairs on the compound eyes. The last tarsal joint of every leg bears a pair of notched claws which enable the bee to obtain a foothold on rough surfaces. Between the claws is a fleshy glandular lobule, the *pulvillus*, whose sticky secretion makes it possible for the bee to cling to smooth objects. Tactile hairs are also present.

The middle, or *mesothoracic legs*, are provided with a *pollen brush*, but, instead of an antenna cleaner, a *spur* is present at the

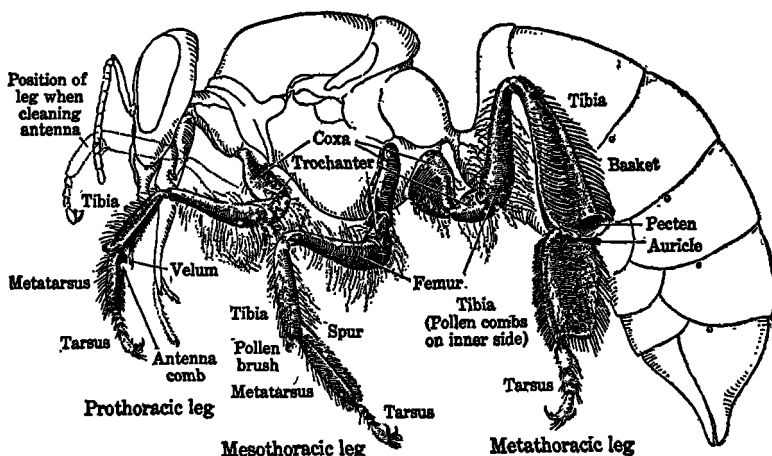


FIG. 363. — Legs of the honeybee. (From Woodruff.)

distal end of the tibia. This spur is used to pry the pollen out of the pollen baskets on the third pair of legs, and to clean the wings.

The *metathoracic legs* possess three very remarkable structures, the pollen basket, the wax pinchers, and the pollen combs. The *pollen basket* consists of a concavity in the outer surface of the tibia with rows of curved bristles along the edges. By storing pollen in this basket-like structure, it is possible for the bee to spend more time in the field, and to carry a larger load at each trip. The pollen combs serve to fill the basket by combing out the pollen, which has become entangled in the hairs on the thorax, and transferring it to the concavity in the tibia of the opposite leg. At the distal end of the tibia is a row of wide spines; these are

opposed by a smooth plate on the proximal end of the metatarsus. The term *wax pinchers* has been applied to these structures, since they are used to remove the wax plates from the abdomen of the worker.

*Sting* (Fig. 364). — The *sting* is a very complicated structure. Before the bee stings, a suitable place is usually selected with

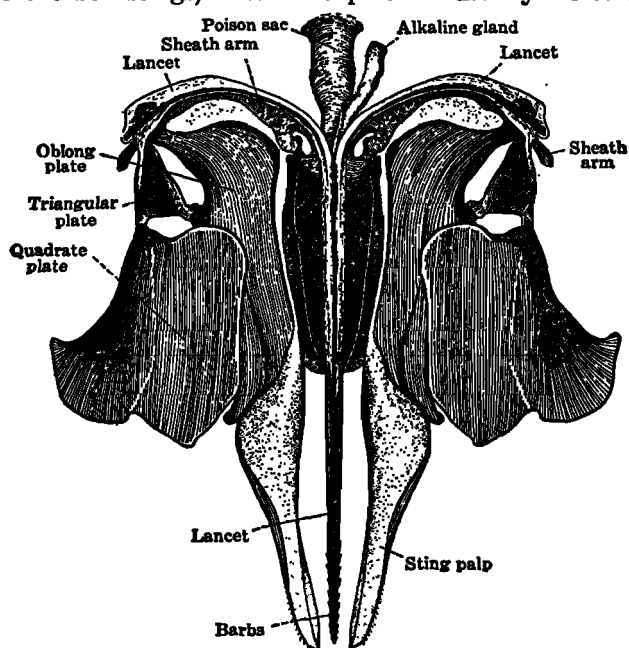


FIG. 364. — Sting of the worker honeybee. (After Snodgrass.)

the help of the *sting feelers*; then the two *barbed darts* are thrust forward. The *sheath* serves to guide the darts, to open up the wound, and to aid in conducting the poison. The *poison* is secreted in a pair of *glands*, one acid, the other alkaline, and is stored in a *reservoir*. Generally the sting, poison glands, and part of the intestine are pulled out when a bee stings, so that death ensues after several hours, but if only the sting is lost, the bee is not fatally injured. The queen seldom uses her sting except in combat with other queens.

## 6. CLASS VI. ARACHNOIDEA

This class contains a number of groups of arthropods some of which have no living representatives. They include the spiders,



ticks, mites, scorpions, and king crabs. These animals differ markedly from one another, but agree in several important respects: (1) they have no antennæ; (2) there are no true jaws; (3) the first pair of appendages are nippers, termed chelicæ; and (4) the body can usually be divided into an anterior part, the cephalothorax, and a posterior part, the abdomen.

These groups are classified by some, as orders in one class, the ARACHNIDA; by others, certain of them are considered classes, or superclasses or subphyla. It seems best to include them all in the class ARACHNOIDEA and arrange them in five subclasses as follows:

**SUBCLASS I. MEROSTOMATA (GIGANTOSTRACA).**

Order 1. XIPHOSURA, king crabs.

Order 2. EURYPTERIDA, Paleozoic only.

**SUBCLASS II. ARACHNIDA.**

Order 1. SCORPIONIDA, scorpions.

Order 2. PEDIPALPI.

Order 3. ARANEIDA, spiders.

Order 4. PALPIGRADI.

Order 5. PSEUDOSCORPIONIDA (CHERNETIDIA.

Order 6. SOLPUGIDA (SOLIFUGÆ).

Order 7. PHALANGIDA, harvestmen.

Order 8. ACARINA, mites and ticks.

**SUBCLASS III. PYCNOGONIDA (PANTOPODA), sea spiders.**

**SUBCLASS IV. TARDIGRADA, water bears.**

**SUBCLASS V. PENTASTOMIDA (LINGUATULIDA).**

**A. Subclass I. Merostomata (Gigantostraca)**

This subclass includes two orders of arthropods that have a cephalothorax (prosoma) consisting of six segments, six pair of laminate, non-locomotor body appendages, and a terminal segment without a caudal fin but with a postanal spine or plate.

**Order 1. XIPHOSURA.** — King or Horseshoe Crabs. Most of the species in this order are extinct. The living king crab, *Limulus polyphemus* (Fig. 365) is a marine animal occurring along the Atlantic coast from Maine to Yucatan. It possesses gills but no Malpighian tubules. *Limulus* is a burrowing animal and lives in the sand. It may be active at night, moving by "short swimming hops, the respiratory appendages giving the necessary impetus, whilst between each two short flights the animal balances itself for a

moment on the tip of its tail." The food of *Limulus* consists chiefly of worms, such as *Nereis* (Fig. 202), and mollusks. These are caught while burrowing through the sand, are held by the chelicerae, and chewed by the bases of the walking legs. In the spring the king crabs come near shore to spawn. In some respects the *XIPHOSURA* resemble fossil trilobites and the latter

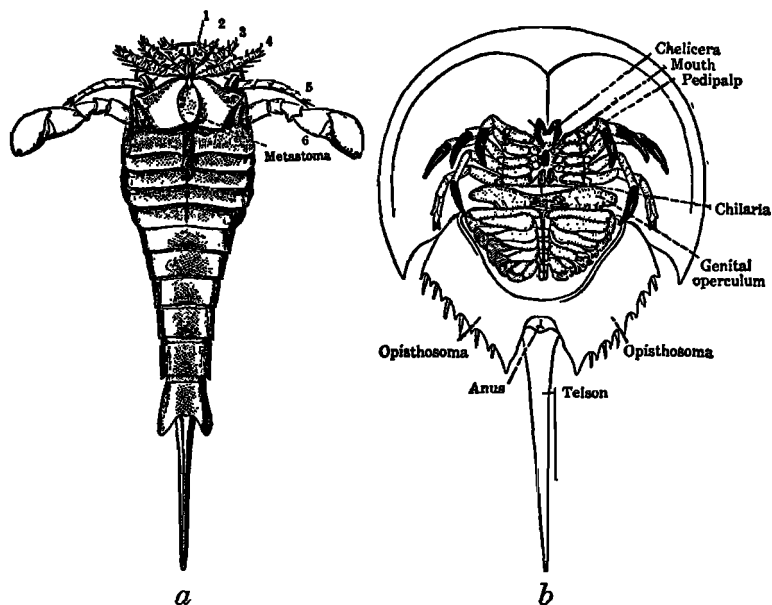


FIG. 365. — MEROSTOMATA. a, EURYPTERIDA; *Eurypterus fischeri*. Restoration of ventral surface from an upper Silurian fossil. 1-6, appendages of prosoma. (After Holm, from Woods.) b, XIPHOSURA; *Limulus polyphemus*, the king or horseshoe "crab." Ventral view. (After Shipley and MacBride, modified.)

are placed by some students near the king crabs in the arthropod series.

**Order 2. EURYPTERIDA** (Fig. 365). — This group is extinct and known only from fossils from Paleozoic strata. They were scorpion-like in appearance with a small cephalothorax and an abdomen of twelve segments, the anterior six of which were provided with unbranched, plate-like appendages. The largest arthropods known belonged to this order, having reached a length of over six feet. Ex. *Eurypterus*, *Pterygotus*, *Stylomurus*.

# B. Subclass II. Arachnida

The ARACHNIDA include the spiders, scorpions, mites, etc. These animals have no antennæ nor true jaws; the first pair of appendages are chelicerae; and a cephalothorax, and abdomen are evident. Eight orders are described here following a more detailed account of the spider.

## (1) THE SPIDER

**External features.**—The body of the spider consists of a *cephalothorax* which is undivided, and an *abdomen* which is usually soft, rounded, and unsegmented.

There are six pairs of *appendages* attached to the cephalothorax. Antennæ are absent; their sensory functions are in part performed by the walking legs. The first pair of appendages are called *chelicerae* (Plate VII). They are in many species composed of two parts, a basal "mandible," and a terminal claw. *Poison glands* are situated in the chelicerae. The poison they secrete passes through

a duct and out of the end of the chelicera; it is strong enough to kill insects and to injure larger animals. The second pair of appendages are the *pedipalpi*; their bases, called "maxillæ," are used as jaws to press or chew the food. The pedipalpi of the male are used as copulatory organs.

Following the pedipalpi are four pairs of *walking legs*. This number easily distinguishes spiders from insects, since the latter

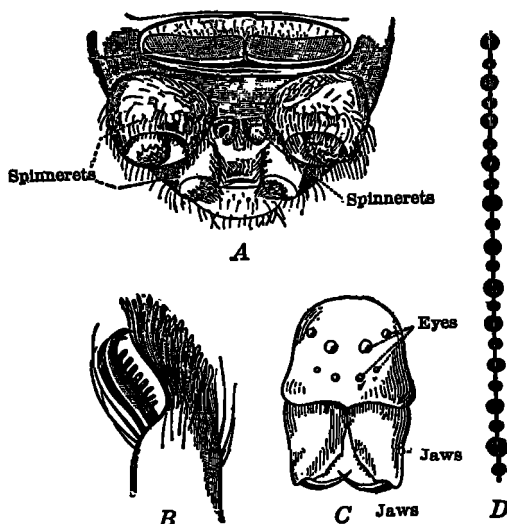


FIG. 366. — Parts of a spider's body. A, ventral view of posterior end of abdomen showing three pairs of spinnerets. B, foot showing claws and bristles. C, front of head showing eyes and jaws. D, a thread from a spider's web. (From Warburton.)

possess only three pairs. Each leg consists of seven joints, — (1) coxa, (2) trochanter, (3) femur, (4) patella, (5) tibia, (6) metatarsus, (7) tarsus, — and is terminated by two toothed claws (Fig. 366, *B*) and often a pad of hairs which enables the spider to run on ceilings and walls. The bases of certain of the legs sometimes serve as jaws.

The *sternum* lies between the legs, and a “*labium*” is situated between the “*maxillæ*.” The *eyes*, usually eight in number, are

on the front of the head (Fig. 366, *C*). The *mouth* (Plate VII) is a minute opening between the bases of the pedipalpi (*maxillæ*); it serves for the ingestion of juices only, since spiders do not eat solid food.

The *abdomen* is connected by a slender waist with the cephalothorax. Near the anterior end of the abdomen on the ventral surface is the *genital opening*, protected by a pair of appendages which have fused together to form a plate called the *epigynum*. On either side of the epigynum is the slit-like opening of the respiratory organs or *lung books* (Fig. 367). Some spiders also possess *tracheæ*

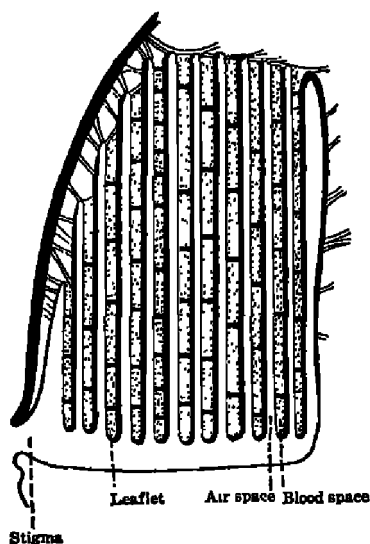


FIG. 367. — Spider. Lung book, longitudinal section. (After MacLeod, modified.)

which open to the outside near the posterior end of the ventral surface (Plate VII). Just back of the tracheal opening are three pairs of tubercles or *spinnerets* (Fig. 366, *A*), used for spinning threads. The *anus* lies posterior to the spinnerets.

**Internal anatomy and physiology** (Plate VII). — The *food* of the spider consists of juices sucked from the bodies of other animals, principally insects. Suction is produced by the enlargement of the sucking stomach, due to the contraction of muscles attached to its dorsal surface and to the chitinous covering of the cephalothorax. The *true stomach*, which follows the sucking stom-

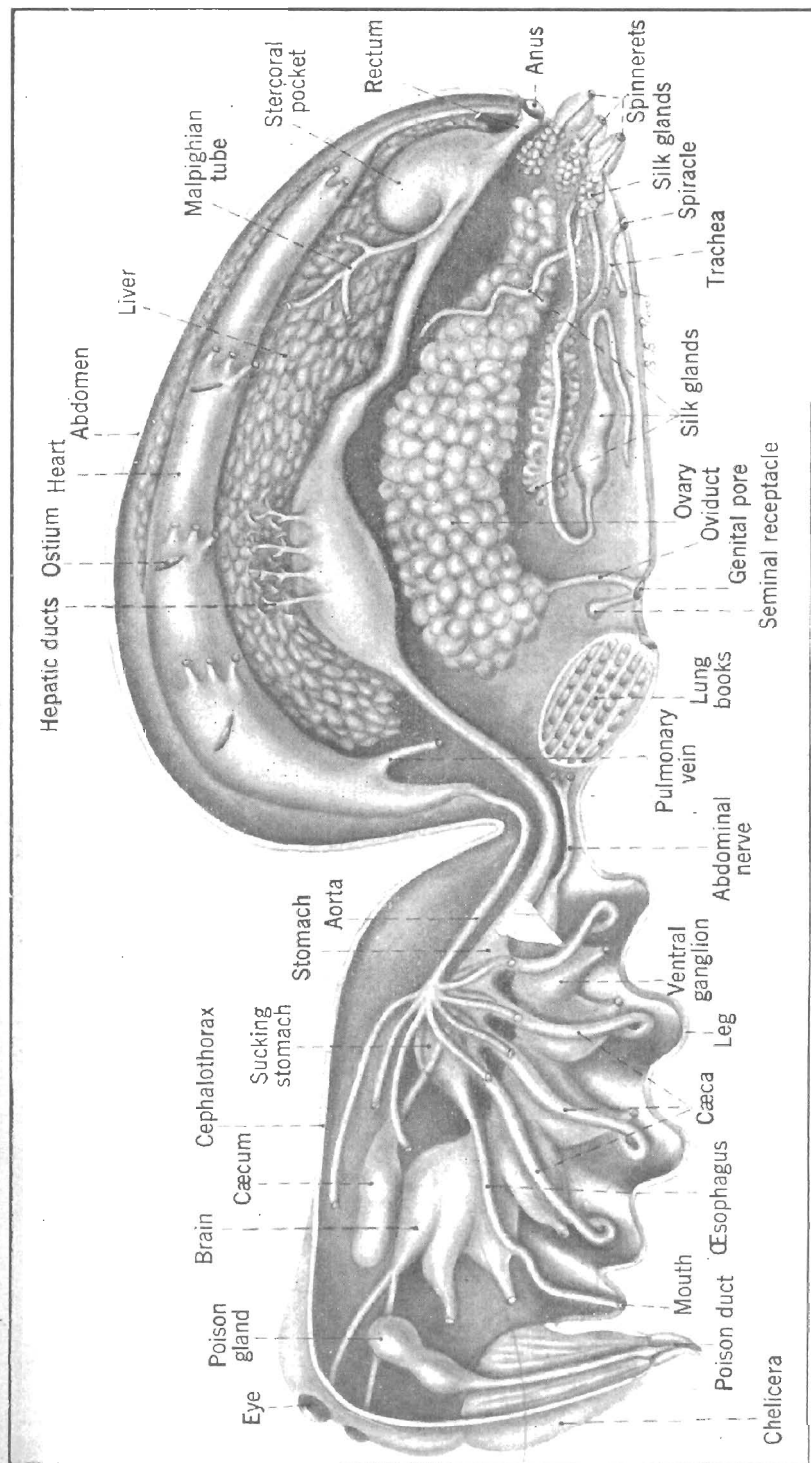


PLATE VII. Longitudinal section of a Spider showing internal organs. (Drawn by Barbara Bradley Root.)

ach, gives off five pairs of *ceca* or blind tubes in the cephalothorax. The *intestine* passes almost straight through the abdomen; it is enlarged at a point where ducts bring into it a digestive fluid from the "*liver*," and again near the posterior end, where it forms a sac, the "*stercoral pocket*." Tubes, called *Malpighian tubes*, enter the intestine near the posterior end. The alimentary canal is surrounded in the abdomen by a large digestive gland or "*liver*." This gland secretes a fluid resembling pancreatic juice and pours it into the intestine through ducts.

The *circulatory system* consists of a heart, arteries, veins, and a number of spaces or sinuses. The *heart* is situated in the abdomen and is surrounded by the digestive glands. It is a muscular, contractile tube lying in a sheath, the pericardium, into which it opens by three pairs of ostia. It gives off posteriorly a caudal artery, anteriorly an aorta which branches and supplies the tissues in the cephalothorax, and three pairs of abdominal arteries. The *blood*, which is colorless and contains mostly amœboid corpuscles, passes from the arteries into sinuses and is carried to the book lungs where it is aerated; it then passes to the pericardium by way of the pulmonary veins, and finally enters the heart through the ostia.

*Respiration* is carried on by tracheæ and book lungs; the latter are peculiar to arachnids. The *book lungs*, of which there are usually two, are sacs, each containing generally from fifteen to twenty leaf-like horizontal shelves through which the blood circulates. Air entering through the external openings is thus brought into close relationship with the blood. Tracheæ are also usually present, but do not ramify to all parts of the body as in the insects (Fig. 297).

The *excretory organs* are the *Malpighian tubules*, which open into the intestine, and two *coxal glands* in the cephalothorax. The coxal glands are sometimes degenerate, and their openings are difficult to find; they are homologous with the green glands of the crayfish (Plate V).

The *nervous system* consists of a bilobed ganglion above the œsophagus, a subœsophageal ganglionic mass and the nerves which arise from them. There are *sensory hairs* on the pedipalps and probably on the walking legs, but the principal sense organs are the eyes. There are usually eight *eyes* (Fig. 366, C), and these differ in size and arrangement in different species. Spiders ap-

parently can see objects distinctly only at a distance of four or five inches.

The sexes are separate, and the *testes* or *ovaries* form a network of tubes in the abdomen. The spermatozoa are transferred by the pedipalps of the male to the female, and fertilize the eggs within her body. The eggs are laid in a silk cocoon, which is attached to the web or to a plant, or carried about by the female.

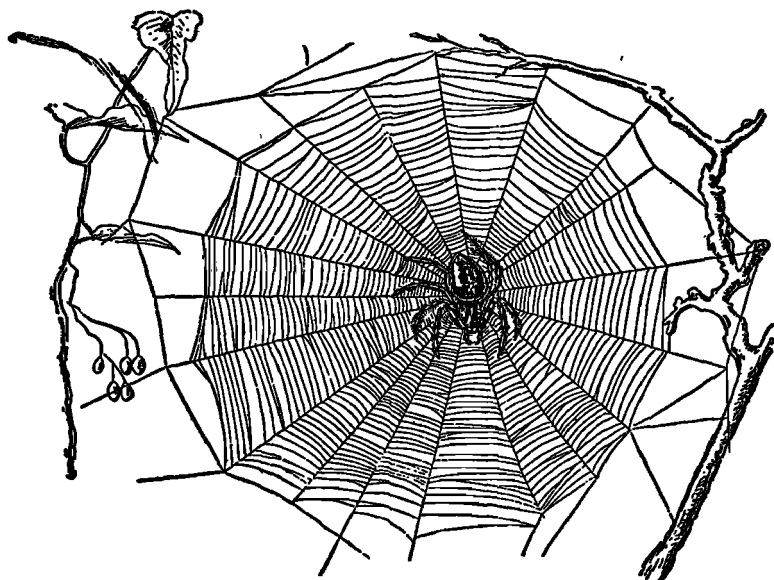


FIG. 368. — Web of the garden spider. (After Blanchard.)

The young leave the cocoon as soon after hatching as they can run about.

The *spinning organs* of spiders are three pairs of appendages called *spinnerets* (Fig. 366, A). The spinnerets are pierced by hundreds of microscopic tubes through which a fluid secreted by a number of abdominal *silk glands* (Plate VII), passes to the outside and hardens in the air, forming a thread. These threads are used to build nests, form cocoons, spin webs, and for many other purposes. An *orb web*, such as is shown in figure 368, is spun in the following manner. A thread is stretched across the space selected for the web; then from a point on this thread other threads are drawn out and attached in radiating lines. These threads all become dry and smooth. On this foundation a spiral

is spun of sticky thread. The spider stands in the center of the web or retires to a nest at one side and waits for an insect to become entangled in the sticky thread; it then rushes out and spins threads about its prey until all struggles cease.

Many spiders do not spin webs, but wander about capturing insects, or lie in wait for them in some place of concealment. In this group belong the crab-spiders (*THOMISIDÆ*, Fig. 371, *D*), jumping-spiders (*ATTIDÆ*, *G*, *J*), ground-spiders (*DRASSIDÆ*), and running spiders (*LYCOSIDÆ*, *H*). The cobweb spiders spin various kinds of nets for capturing insects. The tube-weavers (*AGELENIDÆ*) build platforms on the grass and hide in a tube at one side.

## (2) OTHER ARACHNIDA

**Order 1. SCORPIONIDA.** — The scorpions (Fig. 369) are rapacious arachnids measuring from half an inch to eight inches in length.

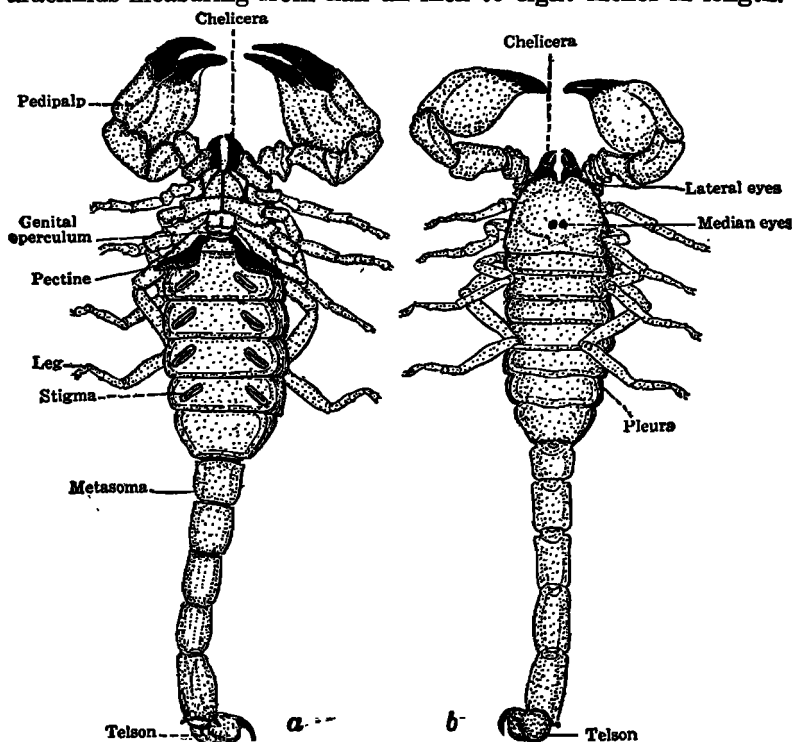


FIG. 369. — SCORPIONIDEA. Scorpion. a, Ventral view. b, Dorsal view.  
(After Shipley and MacBride, modified.)



They live in tropical and subtropical regions, hiding in crevices or in pits in the sand during the daytime, but running about actively at night. They capture insects and spiders with their pedipalpi, tear them apart with their chelicerae, and devour the pieces. Larger animals are paralyzed by the sting on the end of the tail. This sting does not serve as a weapon of defense unless the scorpion is hard pressed; and is not used, as is often stated, to sting itself to death, since its poison has no effect upon its own body.

The scorpion's body is more obviously segmented than that of most of the other arachnids. There is a *cephalothorax* (pro-

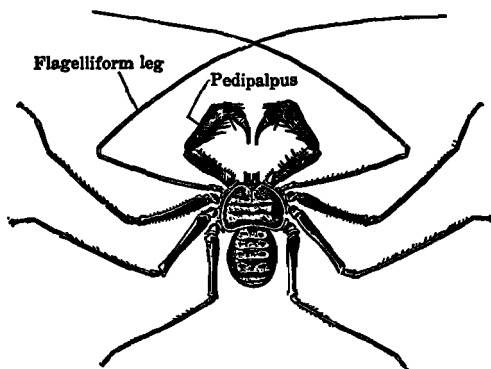


FIG. 370. — PEDIPALPI. *Admetus pumilio*.  
(From Sedgwick.)

soma), and an abdomen of two parts — a thick anterior portion (mesosoma), and a slender tail (metasoma) which is held over the back when the animal walks.

The dorsal shield of the cephalothorax bears a pair of median eyes and three lateral eyes on each side. The sense of sight is, however, poorly developed. On the ven-

tral surface of the second abdominal segment are two comb-like appendages called pectines; these are probably special tactile organs. *Tactile hairs* are distributed over the body, and the sense of touch is quite delicate. There are four pairs of *lung books* opening by means of *stigmata* on the undersurface of abdominal segments III–VI.

The mating activities of scorpions are very curious, and include a sort of promenade. Scorpions are viviparous. The young ride about upon the back of the female for about a week, and then shift for themselves. They reach maturity in about five years.

Family 1. SCORPIONIDÆ. — Ex. *Diplocentrus whitei*: about 5 cm. long; Texas to California.

Family 2. VEJOVIDÆ. — Ex. *Vejovis mexicanus*: about 8 cm. long; Texas.

**Order 2. PEDIPALPI.** — The members of this order have large, conspicuous pedipalps. They are nocturnal in habit and live in damp places under stones and in crevices during the day. They inhabit warm countries and feed chiefly on insects. The PEDIPALPI are not poisonous, although when handled they emit a pungent, acrid secretion of value for defensive purposes. The first pair of legs are long and slender with many segments and serve as tactile organs.

Family 1. THELYPHONIDÆ. — Whip scorpions; with long, slender tail. Ex. *Mastigoproctus giganteus*: vinegar roach; about 13 cm. long; emits odor of vinegar; Florida to Arizona.

Family 2. TARANTULIDÆ. — Body broad; no long, slender tail. Ex. *Tarantula whitei*: about 2 cm. long; Texas to California.

Family 3. HUBBARDIIDÆ. — Palpi not chelate. Ex. *Trithyreus pentapeltis*: about 1 cm. long; southern California.

**Order 3. ARANEIDA.** — Some of the families of ARANEIDA are as follows:

Family 1. AVICULARIIDÆ (Fig. 371, A). — Tarantulas and trap-door spiders; 2 pairs of lungs; 8 eyes; chelicerae move up and down. Ex. *Eurypelma hentzi*: tarantula; large; southwestern states. *Pachylomerus audonini*: trap-door spider; lives in cylindrical hole in ground that can be closed by hinged earthen door.

Family 2. AGELENIDÆ. — Funnel-web spiders; legs long; feet with 3 claws; posterior spinnerets long; 8 eyes in 2 rows. Ex. *Agelena navia*: grass spider; web concave with funnel-shaped tube at side. *Argyroneta aquatica*: European aquatic spider; lives at bottom of ponds among plants; air carried down from surface.

Family 3. THERIDIIDÆ (Fig. 371, B, C, I). — Comb-footed weavers; tarsi of posterior legs with comb of curved, toothed setae. Ex. *Theridion tepidariorum* (Fig. 371, I): common house spider; irregular web in corners, etc.

Family 4. ARGIOPIDÆ (Fig. 371, E, F). — Orb weavers; tarsi clothed with hairs; 3 claws on feet; 8 eyes; web (Fig. 369). Ex. *Epeira foliata*: common on vegetation and fences.

Family 5. THOMISIDÆ (Fig. 371, D). — Crab spiders; short, flat, and crab-like; 2 claws on feet; 8 eyes in 2 rows. Ex. *Misumenavatia*: frequents flowers; no web; color may change from white to yellow according to color of flower.

Family 6. LYCOSIDÆ (Fig. 371, H). — Running or wolf spiders; body long, hairy; 8 eyes in 3 rows, larger eyes on posterior row;

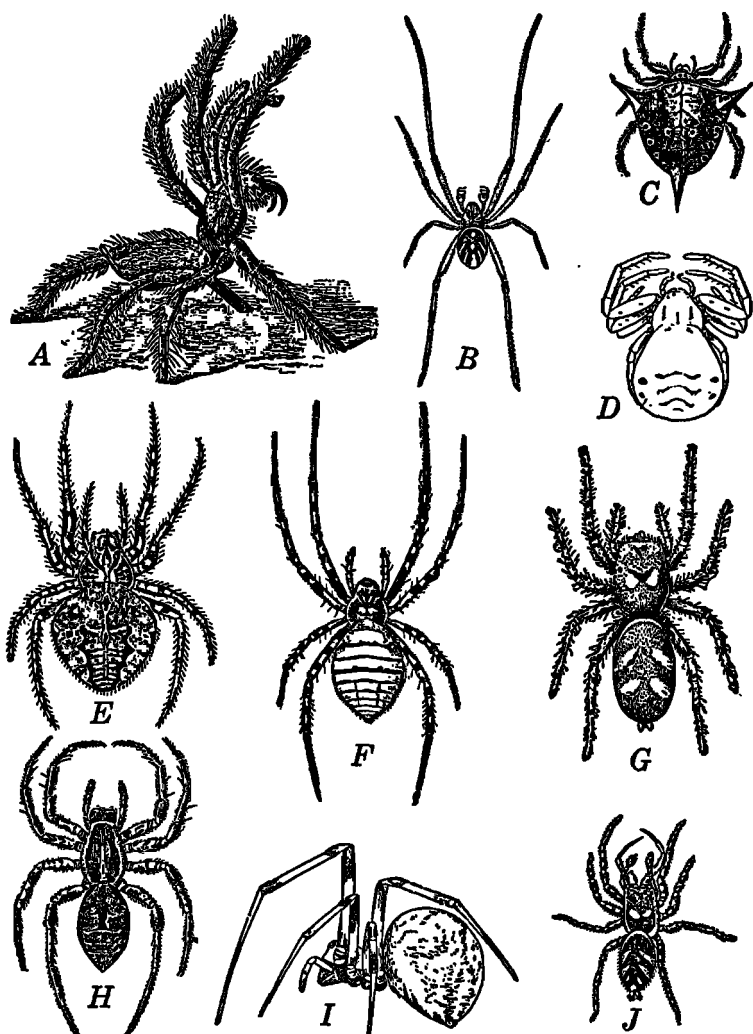


FIG. 371. — ARANEIDA. Species belonging to various families. A, AVICULARIIDÆ; *Chilobrachys stridulans*. B, THERIDIIDÆ; *Latrodectus mactans*. C, THERIDIIDÆ; *Trithena tricuspida*. D, THOMISIDÆ; *Thomisus*, a crab spider. E, ARGIOPIDÆ; *Epeira angulata*. F, ARGIOPIDÆ; *Argiope aurelia*. G, ATTIDÆ; *Attus*, a jumping spider. H, LYCOSIDÆ; *Lycosa fabrilis*. I, THERIDIIDÆ; *Theridion tepidariorum*. J, ATTIDÆ; *Salticus scenicus*. (From Warburton.)

legs long and stout. Ex. *Lycosa helluo*: no web; cocoon attached to female; young carried on mother's back.

Family 7. **ATTIDÆ** (Fig. 371, *G, J*). — Jumping-spiders; body short; legs stout; no web; can run or jump forwards, backwards,

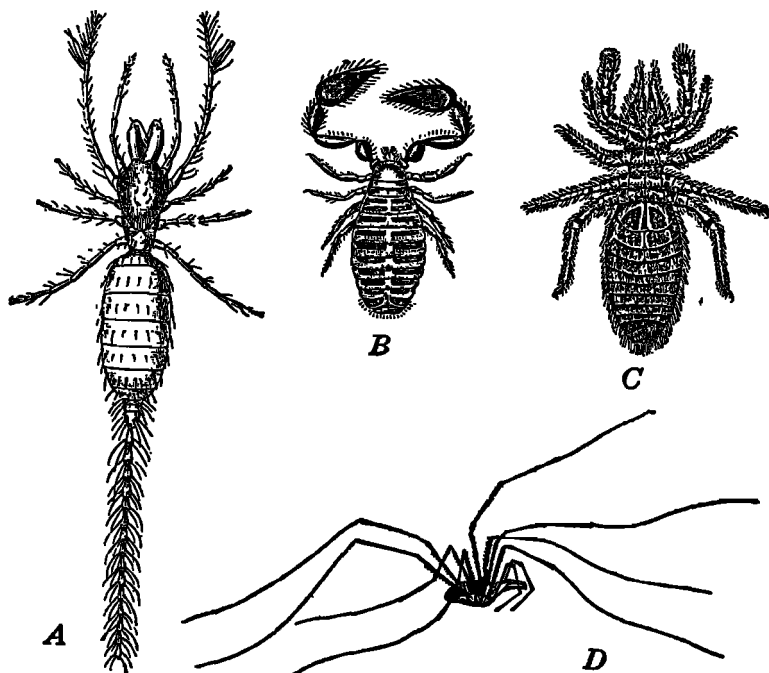


FIG. 372. — ARACHNOIDEA. A, PALPIGRADI; *Kænien mirabilis*. B, PSEUDOSCORPIONIDA; *Chelifer cyrneus*. C, SOLPUGIDA; *Rhagodes*. D, PHALANGIDA; *Phalangium opilio*. (After various authors.)

and sideways. Ex. *Salix scenicus* (Fig. 371, *J*): common on fences and buildings.

**Order 4. PALPIGRADI.** — This order contains a single family, **KÆNENIIDÆ**, and one genus, *Kænien* (Fig. 372, *A*). They possess a long segmented tail and long, slender pedipalps and legs. Ex. *Kænien wheeleri*: about 2.5 mm. long; in moist places under stones; Texas.

**Order 5. PSEUDOSCORPIONIDA (CHERNETIDIA).** — The pseudo-scorpions (Fig. 372, *B*) resemble scorpions in general shape and in the possession of scorpion-like pedipalps but a tail with a caudal sting at the end is lacking. Silk glands are present in the

cephalothorax, opening near the end of the chelicerae. The silk is used to construct nests in which they molt or pass the winter. They live under stones, in moss, under bark, in the nests of termites, ants, and bees, and in houses, and feed on small insects and mites. Large insects to which they cling often carry them about — a fact that probably accounts for their wide distribution.

Family 1. CHELIFERIDÆ. — Ex. *Chelifer cancroides*: book scorpion; about 3 mm. long; in books, furniture, and clothing; cosmopolitan.

Family 2. OBISIDÆ. — Ex. *Chthonius pennsylvanicus*: about 1.9 mm. long; eastern United States.

Order 6. SOLPUGIDA (SOLIFUGÆ). — The SOLPUGIDA (Fig. 372, C) live in warm countries in sandy regions. Their large chelate mandibles give them a dangerous appearance but they are not poisonous. Tracheæ are present opening through a pair of spiracles on the thorax and three pairs on the abdomen. Two families are recognized, GALEODIDÆ and SOLPUGIDÆ. Ex. *Eremobates pallipes*: about 13 mm. long; southern states west of Mississippi.

Order 7. PHALANGIDA. — The harvestmen or daddy-long-legs may be distinguished from spiders by their extremely long legs (Fig. 372, D), the absence of a waist, and their segmented abdomen. Tracheæ are present and a single pair of spiracles. There are no silk glands, and hence no web or nest is constructed. Harvestmen are able to run rapidly over leaves and grass. Their food consists of small living insects and the juices of fruit and vegetables. The adults die in the autumn, in the northern part of their range, but their eggs live over winter and hatch in the spring. Ex: *Liobunum vittatum*: body about 9 mm. long; legs from 42 mm. to 90 mm. long; in fields and woods; eastern and central America.

Order 8. ACARINA. — The order ACARINA includes the ticks and mites, most of which are of small size. The head, thorax, and abdomen are fused together forming an unsegmented body. At the anterior end, a small part of the head region is usually segmented off and hinged to the body proper to serve as a movable base for the mouth parts. In some mites the chitinous integument is membranous throughout, in others some portions of the integument are thickened into protective plates or shields. The body and legs usually bear regularly arranged hairs or bristles. ACARINA usually pass through four stages, egg, larva, nymph, and adult. The larva has only three pairs of legs. When it molts to become

a nymph it acquires a fourth pair of legs but still lacks a genital aperture. The nymph, in turn, molts and becomes an adult, with four pairs of legs and a genital aperture.

Mites are extremely numerous both in species and in individuals and are found in all sorts of habitats. Some are ectoparasitic, others endoparasitic on or in all sorts of animals and plants. Some are terrestrial, others live in fresh or salt water. Some feed on

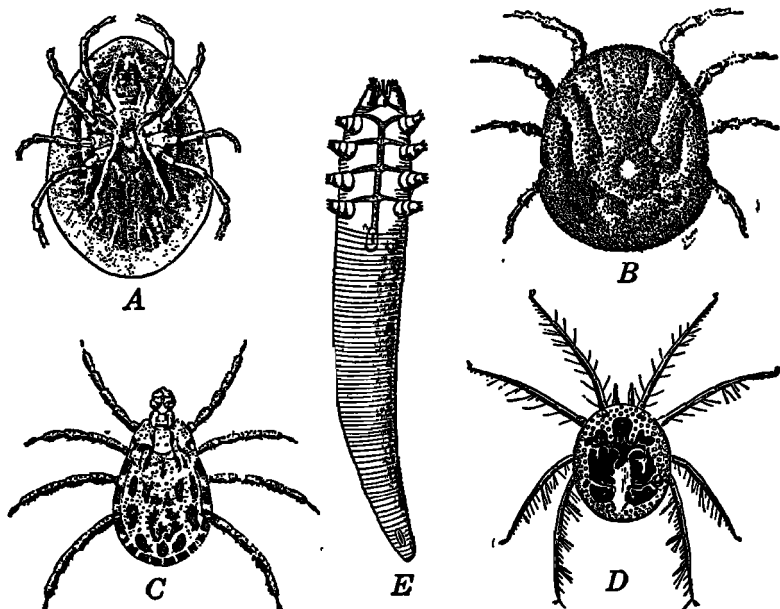


FIG. 373. — ACARINA. A, ARGASIDÆ; *Argas reflexus*, female, ventral view. B, ARGASIDÆ; *Ornithodoros moubata*, male, dorsal view; the vector of tick fever. C, IXODIDÆ; *Dermacentor andersoni*, male, dorsal view; the vector of certain fevers of man. D, HYDRACHNIDÆ; *Atax alticola*, a fresh-water mite. E, DEMODECIDÆ; *Demodex follicularum*, ventral view; the causative agent of "blackheads" in the skin of the human face. (Mostly after Brumpt.)

decaying animal or vegetable matter, others on stored foods, others on plants, others on minute animals, and the parasitic forms on blood.

Family 1. ARGASIDÆ (Fig. 373, A, B). — Soft ticks. The ticks of this family have much the same habits as bedbugs, hiding in cracks or crevices in houses or in the nests of their hosts and coming out at night to feed on the blood of the host for a short period, usually less than half an hour. Ex. *Argas persicus*: para-

sitic on fowls; vector of fowl spirochaetosis; tropics and subtropics. *Ornithodoros moubata* (Fig. 373, *B*): vector of African relapsing fever or tick fever.

Family 2. Ixodidae (Fig. 373, *C*). — Hard ticks. In the hard ticks the two sexes are often very dissimilar in appearance be-

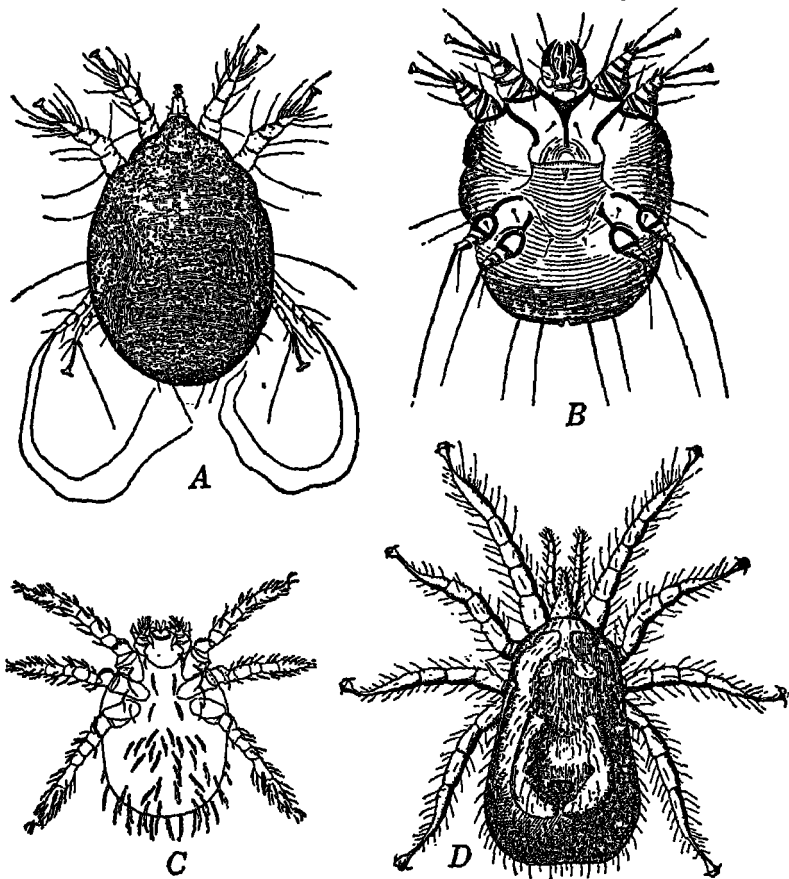


FIG. 374. — ACARINA. A, SARCOPTIDÆ; *Psoroptes ovis communis*; sheep scab mite. B, SARCOPTIDÆ; *Sarcoptes scabiei*, female ventral view; human itch mite. C, TROMBIDIIDÆ; *Trombicula akamushi*, larva with six legs; harvest mite. D, DERMANYSSIDÆ; *Dermanyssus gallinae*, female; chicken mite. (A, after Salmon and Stiles; B, after Gudden; C, D, from Brumpt.)

cause the hard dorsal scutum, which both sexes possess, covers the entire dorsal surface in the male but extends over a small part of the anterior portion of the dorsum of the female. The ticks of

this family attach themselves firmly to their hosts and remain upon them, sucking blood, for days or even weeks. Ex. *Margarus annulatus*: vector of Texas cattle fever. *Hæmaphysalis leporis-palustris*: rabbit tick. *Dermacentor andersoni* (Fig. 373, C); vector of Rocky Mountain spotted fever.

Family 3. ERIOPHYIDÆ. — Gall mites. These mites feed on plant juices and stimulate the formation of galls, the cavities of which open to the outside. *Phyllocoptes pyri*: pear-leaf blister mite.

Family 4. DEMODECIDÆ. — Mites that live in the sebaceous glands and hair follicles of man and domestic animals. Ex. *Dem-*

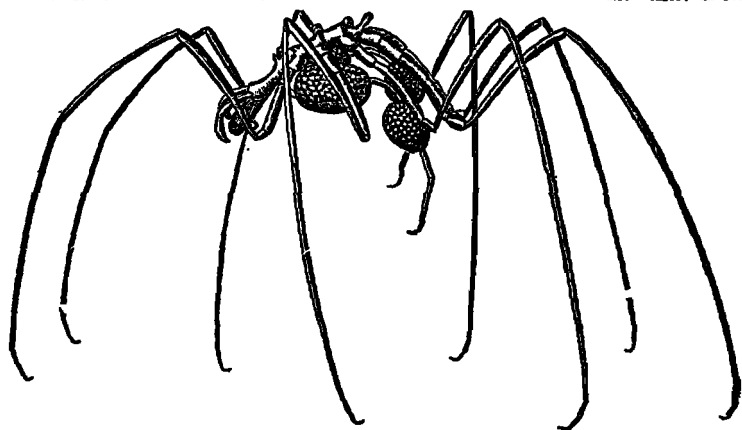


FIG. 375. — PYCNOGONIDA. *Nymphon strömii*; male carrying egg-masses on his ovigerous legs. (From Thompson.)

*odex folliculorum* (Fig. 373, E): parasite of cattle, hogs, and man; causes "blackheads" in skin of human face.

Family 5. DERMANYSSIDÆ. — A number of parasitic species belong to this family. Ex. *Dermanyssus gallinæ* (Fig. 374, D): chicken mite; causes dermatitis in man.

Family 6. SARCOPTIDÆ. — Itch mites. Many parasites of man, mammals, and birds. Ex. *Sarcoptes scabiei* (Fig. 374, B): human itch mite. *Psoroptes ovis communis* (A): sheep scab mite.

Family 7. TROMBIDIDÆ (Fig. 374, C). — Harvest mites and chiggers. Ex. *Trombicula irritans*: North American chigger or red bug. (See also SIPHONAPTERA.)

Family 8. TETRANYCHIDÆ. — Red spiders. Ex. *Tetranychus telarius*: lives on house plants, fruit trees, cotton plants, etc.



Family 9. HYDRACHNIDÆ (Fig. 373, *D*). — Water mites. Ex. *Hydrachna geographica*: adults, dark red; larvæ parasitic on aquatic insects; cosmopolitan.

### C. Subclass III. Pycnogonida (Pantopoda)

The PYCNOGONIDA (Fig. 375) are marine arthropods, sometimes called sea spiders, with very small bodies and disproportionally

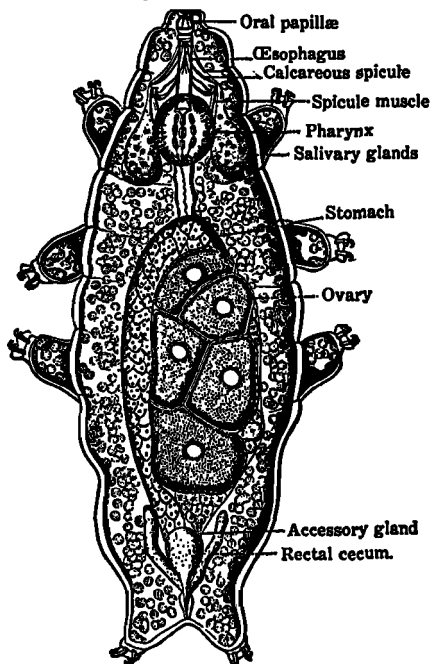


FIG. 376. — TARDIGRADA. *Macrobiotus schultzei*, showing internal anatomy. (From Shipley, after Greeff.)

long legs. They live among algæ and hydroids, on which they feed, and range from one millimeter to several centimeters in length. They are of uncertain systematic position sometimes being placed in a separate class, or in the class CRUSTACEA. The cephalothorax is segmented and the abdomen much reduced; the appendages consist of a pair of long chelate mandibles, a pair of slender pedipalps, a pair of slender ovigerous legs and four pairs of very long legs usually with nine segments each; four eyes are present; long diverticulæ extend from the intestine into the legs; the sexes are separate; the eggs are carried on the ovigerous

legs of the males and give rise to larvæ with three pairs of legs; they are cosmopolitan in their distribution. Ex. *Pycnogonum*, *Pallene*, *Nymphon*.

### D. Subclass IV. Tardigrada

The TARDIGRADA, or water bears (Figs. 376, 377, *B*), are minute animals that are often included with the arachnids although they may not even be arthropods. Here they are given the value of a subclass for the sake of convenience. They live in damp moss or

sand and in fresh water or salt water. The head is more or less distinct and the body consists of four segments fused together. Each body segment bears a pair of short, thick legs which are unsegmented but terminated by from four to nine sharp claws. No circulatory, respiratory, and excretory systems are present.

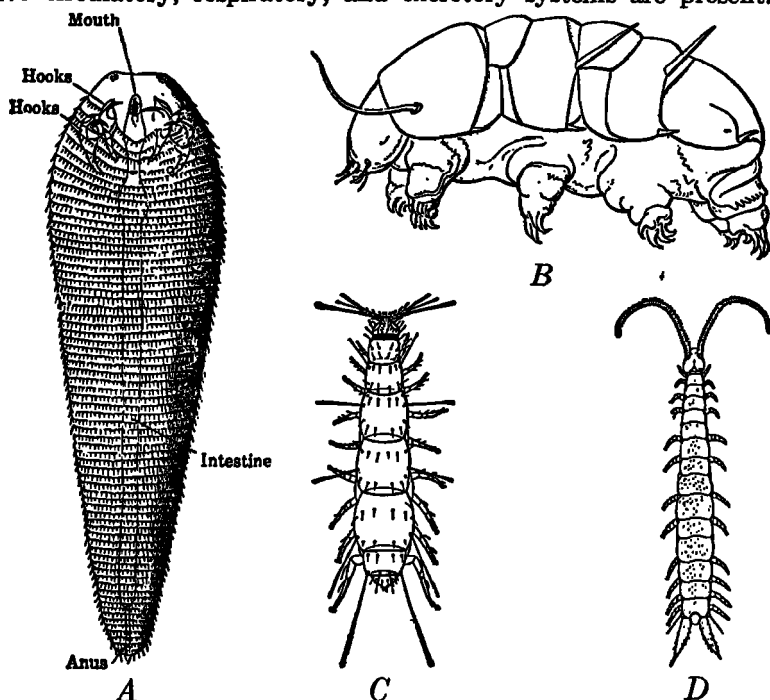


FIG. 377. — A, PENTASTOMIDA; *Linguatula serrata*. B, TARDIGRADA; *Echiniscus spinulosus*. C, PAUROPODA; *Pauropus huxleyi*. D, SYMPHYLLA; *Scutigera immaculata*. (A, from Sedgwick; B, after Doyere; C, D, after Latzel.)

The nervous system, however, is well developed. The sexes are separate. The eggs are large and the young that hatch from them sometimes possess only three pairs of legs. Tardigrades are able to live for several years in a dessicated condition. Two orders are recognized.

**Order 1. EUTARDIGRADA.** — Head without cirri; legs not retractile telescopically; claws united into one branched pair. Ex. *Macrobates hufelandi*: 0.7 mm. long; one pair strong teeth; fresh-water ponds. *Hypsibius*, *Milnesium*.

**Order 2. HETEROTARDIGRADA.** — Head with two pairs of cirri; legs somewhat retractile telescopically; claws separate. Ex. *Echiniscus testudo*: 0.3 mm. long; one pair long teeth; two red eyes; body reddish, opaque; frequent in damp moss on roofs.

### E. Subclass V. Pentastomida (Linguatulida)

The worm-like animals in this subclass are all parasitic. They were formerly grouped with the worms but the morphology of the adults and young prove them to be arthropods allied to the arachnids. The body is unsegmented although the body wall consists of many rings. No circulatory, respiratory, and excretory systems are present. The alimentary canal is straight and close to the mouth is a pair of horny hooks. The sexes are separate. The larvæ have two pairs of legs and are mite-like in shape. Ex. *Reighardia sternæ*: genital opening anterior; hooks posterior to mouth; parasitic in gulls and terns. *Linguatula serrata* (*Pentastomum tæniodes*, Fig. 377, A): female about 8 cm. long; male 2 cm. long; adult in nasal cavities of dog, wolf, and fox; eggs discharged with mucus, when swallowed by rabbits, domesticated animals, or man, hatch in stomach, migrate to lungs, kidneys, etc., and encyst; excyst if host devoured by a carnivore and migrate to nose. *Porocephalus* (*Armillifer*) *armillatus*: adult in lungs of snakes; eggs swallowed by various animals, hatch and larvæ migrate into the liver and body cavity.

## 7. CLASS VII. PAUROPODA

The PAUROPODA, SYMPHYLA, DIPLOPODA, and CHILOPODA are often grouped together in one class, the MYRIAPODA. However, one large group, the CHILOPODA, resembles the insects more than the other large group, the DIPLOPODA; and the two smaller groups, the PAUROPODA and SYMPHYLA have certain characteristics in common with the DIPLOPODA. It seems advisable, therefore, to consider these groups as separate classes. The first three (PAUROPODA, SYMPHYLA, and DIPLOPODA) are sometimes combined into a superclass, the PROGONEATA, characterized by reproductive organs that open to the outside near the anterior end of the body, and the CHILOPODA and INSECTA into a superclass, the OPISTHOGONEATA, with reproductive organs that open near the posterior end.

The PAUROPODA are less than 2 mm. in length. They prey on microscopic animals or eat decaying animal and vegetable matter.

They are without eyes, heart, and special respiratory organs, and evidently breathe through the general surface of the body, as in the earthworm. The head is distinct, and the body contains twelve segments and bears nine pairs of legs. The young possess three pairs of legs when hatched. The two families in this class are the PAUROPIDÆ and EURYPAUROPIDÆ. Ex. *Pauropus huxleyi* (Fig. 377, C): body elongate and cylindrical; 1.3 mm. long; eastern and central United States, Europe. *Eurypauropus spinosus*: body broad and flat; 1.25 mm. long; eastern and central United States, Europe.

### 8. CLASS VIII. SYMPHYLA

The SYMPHYLA are small arthropods with twelve pairs of legs. The head bears antennæ, mandibles, maxillulæ, maxillæ, and a labium. Only one family, the SCOLOPENDRELLIDÆ, two genera, and about twenty-four species belong to the class. They resemble certain wingless insects (THYSANURA, Fig. 311) in habits and appearance, but have a greater number of legs. They live in moist places and avoid light. Their food probably consists of small insects. Ex. *Scutigerebella immaculata* (Fig. 377, D): head distinct; first pair of legs well developed; about 6 mm. long; eastern United States, Europe. *Scolopendrella texana*: head not distinct; first pair of legs rudimentary; 2.8 mm. long; Austin, Texas.

### 9. ARTHROPODS IN GENERAL

The characteristics of each group of arthropods have been presented in the preceding pages, hence it will suffice here to point out in what respects these various groups differ from or resemble each other.

**Anatomy.** — *Divisions of the body.* — The ancestors of the arthropods were probably annelid-like, as in *Peripatus*, which has a muscular body wall and a body that is not divided into well-defined regions. In the CRUSTACEA, INSECTA, CHILOPODA, and DIPLPODA there may be three distinct divisions, head, thorax, and abdomen, or the head and thorax may be united into a cephalothorax. The ARACHNOIDEA usually possess a cephalothorax or prosoma and an abdomen or opisthosoma consisting of the mesosoma and metasoma combined. The size of and number of segments in each of these divisions of the body differ widely within the groups and are correlated with the environment and activities of each species.

*Appendages.* — The paired, jointed appendages, from which the term ARTHROPODA is derived, are of almost infinite variety. Typically each segment bears one pair of appendages but in many species appendages are lacking on many segments. Those that are present were probably derived from a primitive type which has become modified for the numerous functions performed by them. The accompanying table indicates in general the appendages of the larger divisions of the phylum. (Borradaile and Potts.)

*Cuticle.* — The exoskeleton of arthropods consists of chitin often hardened by lime salts. The chitin is inelastic and hence increase in size is impossible except during the period when the exoskeleton is cast off (molting or ecdysis). The new chitin secreted by the hypodermis then allows a certain amount of expansion. The chitin is rigid except between certain segments and joints where it is thin and allows the movement of the adjoining parts.

*Digestive tract.* — The alimentary canal consists of three divisions united end to end. The fore gut or stomodæum and the hind gut or proctodæum are of ectodermal origin, and are lined with chitin which is shed when molting occurs. The mid gut is derived from mesoderm. The length, diameter, and sections into which the various parts of the alimentary canal are divided are correlated with the food habits of the species and vary greatly in the different groups.

*Circulatory system.* — There is, among the arthropods, no complex series of large blood vessels nor fine capillaries that come into direct contact with the tissues; but the circulatory system is of the so-called open type. The blood is contained largely in sinuses and bathes the tissues directly. The movement of the blood is largely due to the expansion and contraction of the body.

*Respiratory system.* — This differs widely in the several divisions of the phylum. In aquatic species respiratory exchanges occur through the general body wall or through well-developed gills or branchiæ. Terrestrial species breathe by means of tracheæ, or, as in the arachnids, by lung books or both lung books and tracheæ.

*Cœlom.* — The "body cavity" of arthropods is not a cœlom but is filled with blood and known as a hæmocœl. The cœlom is represented in the embryo by cavities in the mesodermal segments and in the adult is restricted to the cavities of the reproductive organs and certain excretory organs.

SEGMENTS AND APPENDAGES OF ARTHROPODA

SEGMENT	CRUSTACEA (MALACOSTRACA)	CHILOPODA	ARACHNIDA	INSECTA
1 *	Embryonic	Embryonic		Embryonic
2	Antennules	Antennae	Chelicerae	Antennae
3	Antennae	Embryonic	Pedipalpi	Embryonic
4	Mandibles	Mandibles	1st pair of legs	Mandibles
5	Maxillules	1st maxillae	2d " "	1st maxillae
6	Maxillae	2d "	3d " "	2d "
7	1st maxillipeds	Maxillipeds	4th " "	(Labium)
8	2d thor. append.	1st pair of legs	Embryonic	1st pair of legs
9	3d " "	2d " "	Genital operc. ♀ ♂	2d " "
10	4th " "	3d " "	Pectines	3d " "
11	5th " "	4th " "	1st lung books	1st abd. seg.
12	6th " "	5th " "	2d " "	2d " "
13	7th " "	6th " "	3d " "	3d " "
14	8th " "	7th " "	4th " "	4th " "
15	1st abd. append.	8th " "	No appendages	5th " "
16	2d " "	9th " "	1st seg. Metasoma	6th " "
17	3d " "	10th " "	2d " "	7th " "
18	4th " "	11th " "	3d " "	8th " "
19	5th " "	12th " "	4th " "	9th " " (style) ♂
20	6th " "	13th " "	5th " "	10th " "
21	...	14th " "	...	11th " " (cerci)
22	...	15th " "	...	...
23	...	16th " "	...	...
24	...	17th " "	...	...
25	...	18th " "	...	...
26	...	19th " "	...	...
27	...	20th " "	...	...
28	...	21st " "	...	...
29	...	Genital append. ♀ ♂	...	...
Postseg- mental region	Telson	Telson	Telson	Embryonic

\* Eyes and frontal organs belong to a presegmental region which may have mesoblast of its own.  
♂ indicates the position of the male opening, ♀ that of the female.

*Excretory system.* — There are no true nephridia among the arthropods. Malpighian tubules are present in insects, chilopods, diplopods, and arachnids and some arthropods possess coelomoducts.

*Nervous system.* — This is probably derived from an ancestral condition in which a double ventral nerve cord with a pair of ganglia in each segment was present. In the arthropods of to-day there is a brain and more or less shortened ventral nerve chain. The brain consists of several pairs of ganglia fused together, and may exhibit several divisions known as the fore brain, mid brain, and hind brain (Fig. 300). The ventral nerve cord likewise usually consists of a reduced number of masses of nervous tissue each comprising several pairs of ganglia.

*Eyes.* — In *Peripatus* the eyes are a pair of simple, closed vesicles with a lens derived from the wall and a thickened, pigmented posterior complex. In all other arthropods the lens is derived from the cuticula; beneath the lens are cells known as retinulæ, in each of which is a vertical rod called the rhabdom; and in and around the retinulæ is pigment which may migrate toward or away from the surface according to the intensity of the light. The simple eyes of insects (ocelli) consist of a single vesicle with several retinulæ. In chilopods and diplopods a number of vesicles lie close together in a group. The compound eyes of crustaceans and insects are very complex structures the units of which are known as ommatidia. The arachnids possess eyes that resemble the ocelli of insects but are probably degenerate compound eyes.

*Phylogeny and interrelations.* — The arthropods no doubt evolved from the same ancestors as the polychæte annelids. The development of a rigid exoskeleton with joints brought about a change in the distribution of the muscles from the continuous type forming a muscular body wall, as in the annelids, to the discontinuous type in which the muscles are separately and diversely developed for the movement of special segments.

The ONYCHOPHORA resemble most closely the ancestral condition, with a thin cuticle, a continuous and muscular body wall, no joints, one pair of jaws, appendages on the first segment, and a series of coelomoducts of which one pair are ciliated oviducts.

The CRUSTACEA, INSECTA, CHILOPODA, and DIPLOPODA have become modified in many ways. The CRUSTACEA differ from the others in the possession of a second pair of antennæ and in their

aquatic habit. The INSECTA have only three pairs of legs and usually wings. Both CRUSTACEA and INSECTA possess compound eyes. The ARACHNOIDEA have anterior appendages modified into chelicerae and lack true compound eyes.

**History of our knowledge of the Arthropoda.** — The term ARTHROPODA was proposed by von Siebold in 1845 for a group of animals including the CRUSTACEA, INSECTA, and ARACHNIDA. This group resembled the ARTICULATA of Cuvier except that the ANNELIDA were removed and placed with the VERMES. Linnæus employed INSECTA as a term for all of the arthropods; but separate classes later were recognized, the MYRIAPODA by Latreille in 1796, the CRUSTACEA by Cuvier in 1800, and the ARACHNIDA by Lamarck in 1881. Many changes of comparatively minor importance have taken place since that time and are still being made, a condition that indicates both our lack of knowledge of certain sections of the phylum and the fact that we are making progress.

**Embryology and the biogenetic law.** — Studies of the embryology of arthropods has furnished some of our best evidence in favor of what is known as the biogenetic law or the *recapitulation theory*. Organic evolution, that is, the evolution of one organism from another, is accepted as an established fact by practically all zoologists at the present time. Evolutionists do not claim that the more complex forms have evolved directly from the simpler animals, but that their ancestors were related. Beginning with the simplest animals we find that a single cell performs all the necessary processes of life, *e.g.* *Amæba*. Within the lowest phylum, the PROTOZOA, there are animals consisting of a number of cells more or less intimately bound together into a hollow spherical colony, *e.g.* *Volvox*. Passing to the next higher group of organisms we are introduced to animals that possess two layers of cells, surrounding a single cavity, *e.g.* *Hydra*. All animals above the coelenterates have three layers of cells forming their body walls, *i.e.* are triploblastic. Four stages in the evolution of animals are represented in the groups just mentioned — (1) the single cell, (2) a ball of cells, (3) a two-layered sac, and (4) a three-layered organism.

Early in the past century it was noticed that these stages correspond to the early stages in the embryology of the METAZOA; in other words, that the development of the individual recapitulates the stages in the evolution of the race, or *ontogeny recapitulates phylogeny*. These stages contrasted appear as follows: —



<i>Phylogenetic Stage</i>	<i>Ontogenetic Stage</i>
(1) single-celled animal	egg cell
(2) ball of cells	blastula
(3) two-layered sac	gastrula
(4) triploblastic animal	three-layered embryo

Later other zoologists became interested in the recapitulation theory, and enlarged upon it. Of these Fritz Müller and Ernst Haeckel are especially worthy of mention. The latter expressed the facts as he saw them in his "fundamental law of biogenesis." The ancestor of the many-celled animals was conceived by him as a two-layered sac something like a gastrula, which he called a *Gastræa*. The coelenterates were considered to be *gastræa* slightly modified.

Fritz Müller derived strong arguments in favor of biogenesis from a study of certain CRUSTACEA belonging to the MALACOSTRACA. Many members of this group do not emerge from the egg so nearly like the adult as does the crayfish. The lobster, for example, upon hatching resembles a less specialized prawn-like crustacean, called *Mysis* (Fig. 277, c), and is said to be in the *Mysis* stage. The shrimp, *Penæus*, passes through a number of interesting stages before the adult condition is attained. It hatches as a larva, termed a *Nauplius* (Fig. 378, A), possessing a frontal eye and three pairs of appendages; this *Nauplius* molts and grows into a *Protozoæa* stage (B) which bears three more pairs of appendages and the rudiments of segments III-VIII. The *Protozoæa* stage grows into the *Zoæa* stage (C). The cephalothorax and abdomen are distinct at this time; eight pairs of appendages are present (I-VIII) and six more are developing. The *Zoæa* grows and molts and becomes a *Mysis* (D) with eight pairs of appendages (I-VIII) on the cephalothorax. Finally the *Mysis* passes into the adult shrimp, which possesses the characteristic number of appendages (I-XIX) each modified to perform its particular function. The *Nauplius* of *Penæus* resembles the larvæ of many simple crustaceans; the *Zoæa* is somewhat similar to the condition of an adult *Cyclops* (Fig. 274, a); the *Mysis* is like the adult *Mysis* (Fig. 277, c); and finally the adult *Penæus* is more specialized than any of its larval stages, and belongs among the higher CRUSTACEA. The above facts have convinced some zoologists that *Penæus* recapitulates in its larval development the progress of the race; that the lobster has lost many of these stages, retaining only the *Mysis*; and that

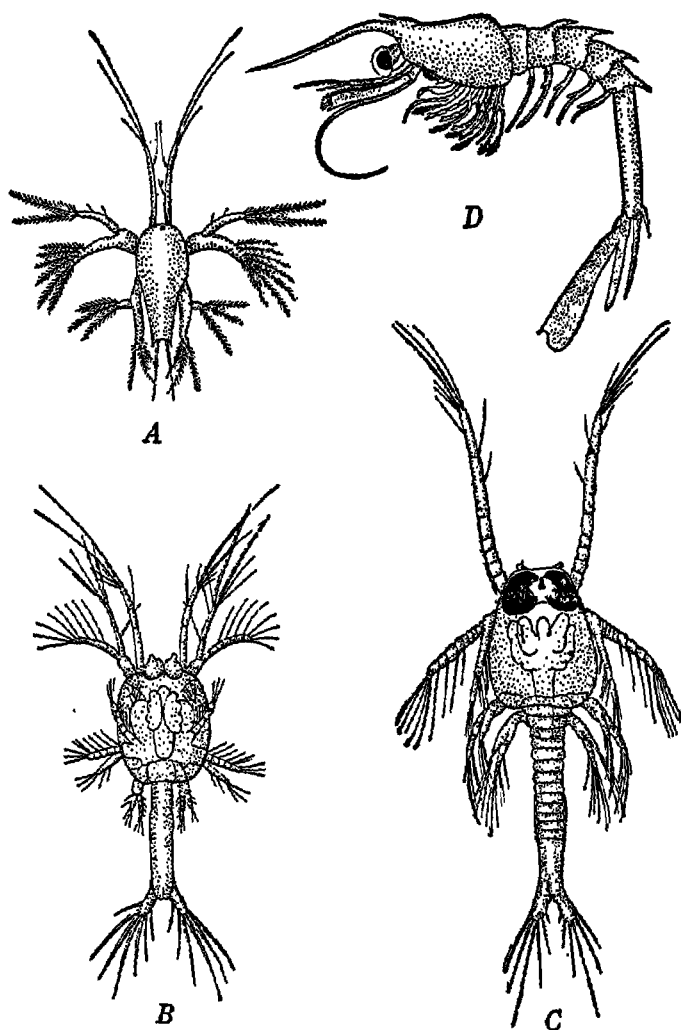


FIG. 378. — Four stages in the development of *Penaeus*, a shrimp. A, *Nauplius*; B, *Protozoa*; C, *Zoea*; D, *Mysis*. (After Müller and Claus.)

the crayfish hatches in practically the adult condition. The *Nauplius* stage of the latter is supposed to be represented by a certain embryonic phase (Fig. 271, *E*).

The law of biogenesis should not be taken too seriously, since it has been criticized severely by many prominent zoologists, but it has furnished an hypothesis, which has concentrated the attention of scientists upon fundamental embryological processes, and has therefore had a great influence upon zoological progress.

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## CHAPTER XI

### PHYLUM ECHINODERMATA

#### INTRODUCTION

The echinoderms are the starfishes, brittle-stars, sea-urchins, sea-cucumbers, and sea-lilies. They are coelomate animals, bilaterally symmetrical in the larval stage but radially symmetrical as adults; usually five antimeres are present. A water-vascular system including organs known as tube-feet, is characteristic; also a spiny skeleton of calcareous plates. There are five classes of living echinoderms. Four of these are sometimes grouped together in the subphylum ELEUTHEROZOA because they are able to move about freely; the class CRINOIDEA together with five classes of extinct species comprise the subphylum PELMATOZOA which are stalked and attached during all or part of their lives.

CLASS I. ASTEROIDEA. — Starfishes. Typically pentamerous; arms usually not sharply marked off from the disk; ambulacral groove present. *Asterias forbesi*.

CLASS II. OPHIUROIDEA. — Brittle-stars. Typically pentamerous; arms sharply marked off from the disk; no ambulacral groove. *Ophiura sarsi*.

CLASS III. ECHINOIDEA. — Sea-urchins. Pentamerous, without arms or free rays; test of calcareous plates bearing movable spines. *Strongylocentrotus dröbachiensis*.

CLASS IV. HOLOTHURIOIDEA. — Sea-cucumbers. Long ovoid; muscular body wall; tentacles around mouth. *Thyone briareus*.

CLASS V. CRINOIDEA. — Sea-lilies. Arms generally branched and with pinnules; aboral pole sometimes with cirri but usually with stalk for temporary or permanent attachment. Ex. *Antedon tenella*.

#### 1. CLASS I. ASTEROIDEA

##### (1) ASTERIAS — A STARFISH

**External features.** — The starfishes are common along many seacoasts, where they may be found usually upon the rocks with

the mouth down. The upper surface is therefore *aboral* or *abactinal*. On the *aboral surface* are (1) many *spines* (Fig. 381) of various sizes, (2) *pedicellariæ* (Fig. 380) at the base of the spines, (3) a *madreporite*, which is the entrance to the water-vascular system, and (4) the anal opening (*anus*). A glance at the *oral surface* reveals a *mouth* centrally situated in the membranous *peristome*,

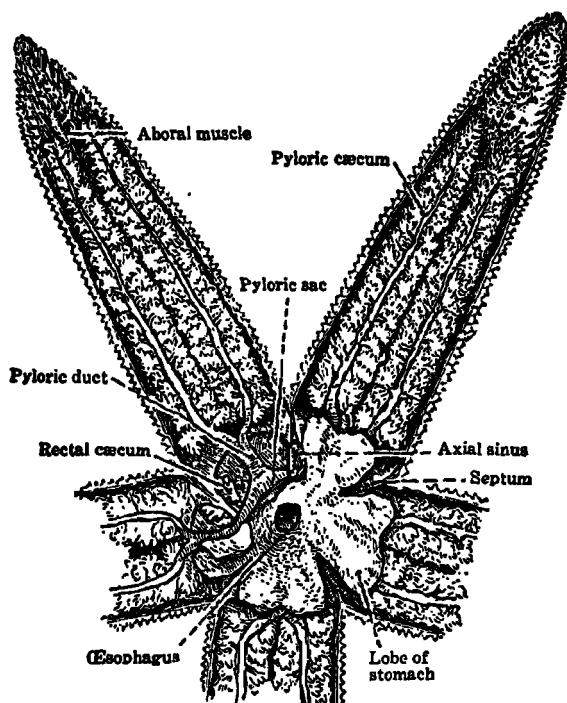


FIG. 379. — Starfish, *Asterias rubens*. Aboral view with two arms and part of skeleton removed; one lobe of stomach cut away and another lobe turned back. (After Borradaile, modified.)

and five *grooves* (*ambulacral*), one in each arm, from which two or four rows of *tube-feet* extend.

**The skeleton.** — The skeleton is made up of *calcareous plates* or *ossicles* bound together by fibers of connective tissue. The ossicles are regularly arranged about the mouth and in the *ambulacral grooves* and often along the sides of the arms, but are more or less scattered elsewhere. The *ambulacral* and *adambulacral ossicles* (Fig. 381) have muscular attachments and are so

situated that when the animal is disturbed they are able to close the groove and thus protect the tube-feet. The *spines* of the starfish are short and blunt and covered with *ectoderm* (Fig. 381). Around their bases are many whitish modified spines called *pedicellariæ* (Fig. 380). These are little jaws which when irritated may be opened and closed by several sets of muscles. Their function is to protect the *dermal branchiæ* (Fig. 381), to prevent débris and small organisms from collecting on the surface, and to capture food. The skeleton serves to give the animal definite

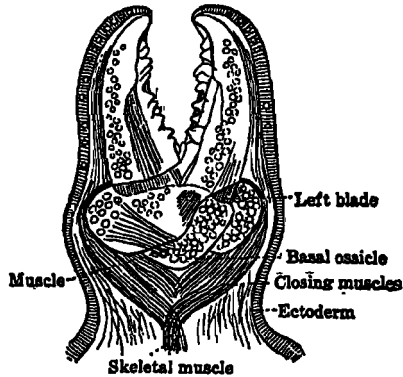


FIG. 380. — Pedicellaria of a starfish. (After Cuenot.)

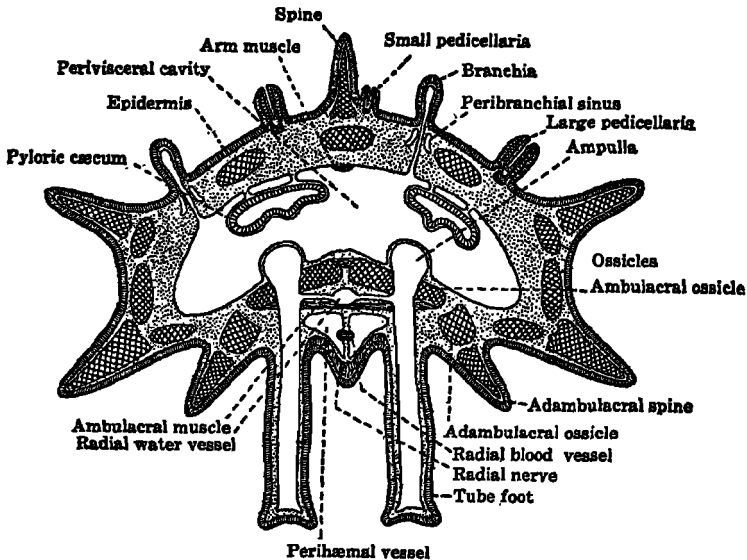


FIG. 381. Diagrammatic transverse section of the arm of a starfish. (From Borradaile and Potts.)

shape, to strengthen the body wall, and as a protection from the action of waves and from other organisms.



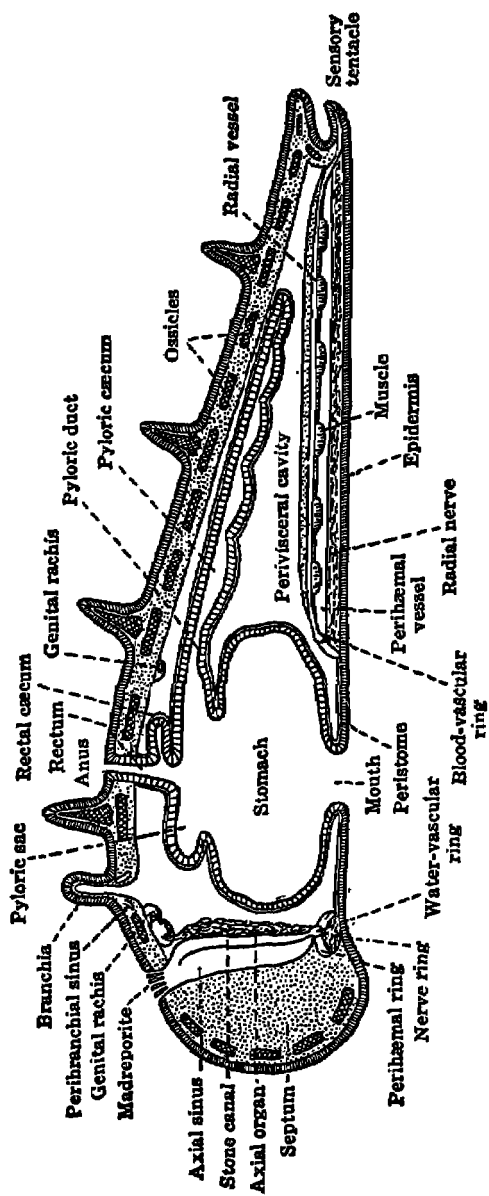


Fig. 382. — Diagrammatic section through the disk and one arm of a starfish. (From Borradaile and Potts.)

**The muscular system.** — The *arms* of the starfish are not rigid, but may be flexed slowly by a few muscle fibers in the body wall (Fig. 381). The *tube-feet* are also supplied with muscle fibers.

**Cœlom.** — The true body cavity of the starfish is very large and may be separated into several distinct divisions. The *perivisceral part of the cœlom* (Figs. 381, 382) surrounds the alimentary canal and extends into the arms. It is lined with *peritoneum* and filled with sea-water containing some albuminous matter. Oxygen is taken into the cœlomic fluid and carbon dioxide given off through outpushings of the body wall known as *papulæ* or *dermal branchiæ*. The cœlom also has an *excretory function*, since cells from the peritoneum are budded off into the cœlomic fluid, where they move about as amœbocytes gathering waste matters. These cells make their way into the dermal branchiæ, through the walls of which they pass to the outside, where they disintegrate.

**The water-vascular system.** — The water-vascular system (Fig. 383) is a division of the cœlom peculiar to echinoderms. Beginning with the *madreporite* the following structures are encountered: the *stone-canal* running downwards enters the *ring-canal*, which encircles the mouth; from this canal five *radial canals* (Fig. 381), one in each arm, pass outward just above the ambulacral grooves. The radial canals give off side branches from which arise the *tube-feet* (Fig. 381) and *ampullæ*. The ampullæ are bulb-like sacs extending into the cœlom; they are connected directly with the tube-feet, which pass through tiny pores between the ambulacral ossicles. Sea water is forced into this system of canals by cilia which occur in grooves on the outer surface of the madreporite and in the canals which penetrate it. Arising from the ring-canal near the ampullæ of the first tube-feet are nine vesicles called, after the name of their discoverer, "Tiedemann's bodies." These structures produce amœbocytes which pass into the fluid of the water-vascular system. *Polian vesicles* (Fig. 383) are present in some starfishes, but not in *Asterias*.

The most interesting structures of the water-vascular system are the *tube-feet* (Figs. 381, 383). They are primarily locomotory and function as follows: "When the tube-foot is to be stretched out, the ampulla contracts and drives the fluid downwards. The contraction of the ampulla is brought about by muscles running circularly around it. The tube-foot is thus distended and its broad flattened end is brought in contact with the surface of the

stone over which it is moving and is pressed close against it. The muscles of the tube-foot itself, which are arranged longitudinally, now commence to act, and the pressure of the water preventing the tearing away of the sucker from the object to which it adheres, the starfish is slowly drawn forward, whilst the fluid in the tube-foot flows back into the ampulla." Tube-feet are also sensory.

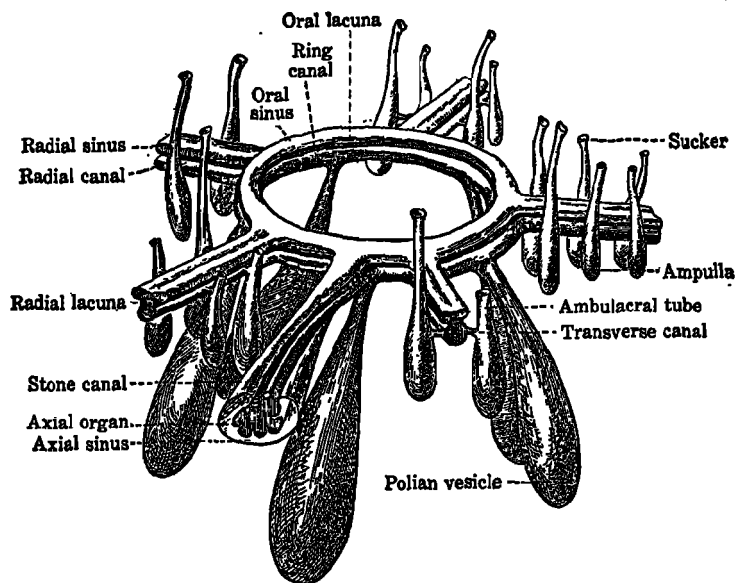


FIG. 383. — Ambulacral system of a starfish. (After Delage and Herouard.)

A number of other spaces and canals have been considered as parts of the coelom and at one time were supposed to be a "blood"-vascular system. These are the *axial sinuses* lying along the stone-canal and opening to the outside through the madreporite, the *inner, circumoral perihæmal canal*, the *outer perihæmal canal* beneath the ring-canal, the *aboral sinus*, and the *peribranchial spaces*. The functions of these various cavities are not clear.

**Digestion.** — The *alimentary canal* of the starfish (Figs. 379, 382) is short and greatly modified. The *mouth* opens into an *œsophagus* which leads into a thin-walled sac, the *stomach*. Following this is the *pyloric sac*. From the pyloric sac a tube passes into each arm, then divides into two branches, each of which possesses a large number of lateral pouches; these branches are called *pyloric* or *hepatic ceca*. They are green in color. Above the

pyloric sac is the slender *rectum*, which may open to the outside through the *anus*. Two branched pouches, brown in color, arise from the rectum and are known as *rectal ceca*.

The *food* of the starfish consists of fish, oysters, mussels, barnacles, clams, snails, worms, Crustacea, etc. When a mussel is to be eaten, the animal seizes it with the tube-feet "and places it directly under its mouth, folding its arms down over it in umbrella fashion. The muscles which run around the arms and disk in the body wall contract, and the pressure thus brought to bear on the incompressible fluid contained in the coelom, forces out the thin membranous peristome and partially turns the stomach inside out. The everted edge of the stomach is wrapped round the prey. Soon the bivalve is forced to relax its muscles and allow the valves to gape. The edge of the stomach is then inserted between the valves and applied directly to the soft parts of the prey, which is thus completely digested. When the starfish moves away, nothing but the cleaned shell is left behind. If the bivalve is small, it may be completely taken into the stomach, and the empty shell later rejected through the mouth." (MacBride.) Schiemenz has shown "(1) that whilst a bivalve may be able to resist a sudden pull of 4000 grammes it will yield to a pull of 900 grammes long continued; (2) that a starfish can exert a pull of 1350 grammes; (3) that a starfish is unable to open a bivalve unless it be allowed to raise itself into a hump so that the pull of the central tube-feet is at right angles to the prey. A starfish confined between two glass plates walked about all day carrying with it a bivalve which it was unable to open." (MacBride.)

The lining of the stomach secretes mucus; that of the pyloric sac and ceca secretes ferments; these change proteids into diffusible peptones, starch into maltose, and fats into fatty acids and glycerine. Thus is digestion accomplished. Undigested matter is ejected through the mouth, and very little, if any, matter passes out of the anus. The rectal ceca secrete a brownish material of unknown function, probably excretory.

**Circulation.** — The fluid in the coelom is kept in motion by cilia and carries the absorbed food to all parts of the body.

**Excretion.** — This is accomplished by the *amœbocytes* (*nephrocytes*) in the coelomic fluid, probably aided by the rectal ceca.

**Respiration.** — The dermal branchiae (Fig. 381) function as respiratory organs.

**The nervous system** (Fig. 382). — Besides many *nerve cells* which lie among the ectoderm cells, there are ridges of nervous tissue, the *radial nerve cords*, running along the ambulacral grooves, and uniting with a *nerve ring* encircling the mouth. The *apical nervous system* consists of a trunk in each arm which meets the other trunks at the center of the disk; these trunks innervate the dorsal muscles of the arms.

**Sense organs.** — The *tube-feet* are the principal sense organs. They receive nerve fibers from the radial nerve cords. At the end of each radial canal the radial nerve cord ends in a *pigmental mass*; this is called the *eye*, since it is a light-perceiving organ. The dermal branchiæ are probably sensory, also.

**Reproduction.** — The *sexes* of starfishes are distinct. The *reproductive organs* are dendritic structures, two in the base of each arm; they discharge the eggs or sperms out into the water through pores in the aboral surface at the interspace between two adjacent arms. The *eggs* of many starfishes are fertilized in the water; they are *holoblastic*, undergo *equal cleavage*, and form a *blastula* and *gastrula* similar to those shown in figure 402. The opening (*blastopore*) of the gastrula becomes the anus, and a new opening, the mouth, breaks through. Ciliated projections develop on either side of the body, and a larva, called a *Bipinnaria* (Fig. 403, C) results. This changes (metamorphosis) into the starfish.

**Behavior.** — The starfish moves from place to place by means of its tube-feet. During the day it usually remains quiet in a crevice, but at night it is most active.

The *responses* of the starfish to *stimuli* are too complex to be stated definitely. When a starfish is placed on its aboral surface it performs the "righting reaction," i.e. it turns a sort of hand-spring by means of its arms. Professor Jennings taught individuals to use a certain arm in turning over. One animal was trained in eighteen days (180 lessons), and after an interval of seven days apparently "remembered" which arm to use. Old individuals could not be trained as readily as young specimens.

**Regeneration.** — The starfish has remarkable powers of regeneration. A single arm with part of the disk will regenerate an entire body. If an arm is injured, it is usually cast off near the base at the fourth or fifth ambulacral ossicle. This is *autotomy*.

## (2) OTHER ASTEROIDEA

The starfishes usually possess 5 arms that are not sharply marked off from the central disk; in some species, however, as many as 40 arms may be present. The body is flattened. They move about with the oral surface down. The viscera extend into the arms and the anus is on the aboral surface. Along the oral surface of each arm is a median ambulacral groove from which

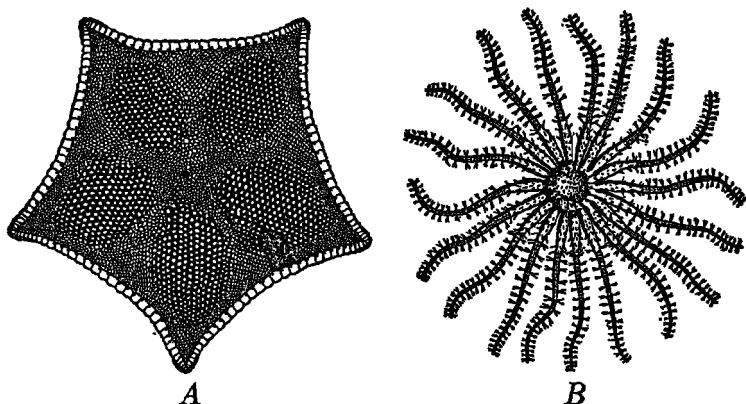


FIG. 384. — ASTEROIDEA. A, *Pentagonaster japonicus*, a type with short arms and pentagonal body. B, *Odinia*, a type with many long arms and small disk. (A, after Sladen; B, after Perrier.)

project either two or four rows of tube-feet. The madreporite is located on the aboral surface between the bases of two of the arms. The outside of the body is covered by a ciliated epithelium and characterized by the presence of spines or tubercles, some of which are movable and others modified into pedicellariæ. The only special sense organs present are a red eye spot at the end of each arm. There are three orders and about twenty families of ASTEROIDEA (Fig. 384).

**Order 1. PHANEROZONIA.**— These have one or two rows of large marginal plates along the arms; 2 rows of tube-feet in each arm; and pedicellariæ, when present, usually sessile or in pits.

**Family 1. ASTROPECTINIDÆ.**— Arms long and slender; paxillæ covering membranous aboral wall; tube-feet conical and without sucking disk; usually no anus. Ex. *Astropecten articulatus*, *Luidia clathrata*.

Family 2. PROCELLANASTERIDÆ. — Arms short; body more or less pentagonal; paxillæ covering membranous aboral wall; no anus; cribriform bodies between certain of the marginal plates. Ex. *Ctenodiscus crispatus*.

Family 3. OREASTERIDÆ. — Body thick; marginal plates small; aboral plates arranged in a reticulum. Ex. *Oreaster reticulatus*.

Order 2. SPINULOSA. — Marginal plates inconspicuous; tube-feet with sucking disks; pedicellariæ pedunculate, usually absent.

Family 1. ASTERINIDÆ. — Body pentagonal; aboral plates granular. Ex. *Asterina miniata*.

Family 2. ECHINASTERIDÆ. — Arms long and slender; no pedicellariæ. Ex. *Echinaster spinulosus*.

Order 3. FORCIPULATA. — Marginal plates inconspicuous; pedicellariæ stalked; prominent spines.

Family 1. STICHASTERIDÆ. — Arms long and slender; 4 rows of tube-feet. Ex. *Stichaster albulus*.

Family 2. ASTERIIDÆ. — Arms often more than 5; disk small; 4 rows tube-feet. Ex. *Asterias forbesi*, *A. vulgaris*.

## 2. CLASS II. OPHIUROIDEA

The brittle-stars and basket-fish (Figs. 385, 388) that belong to this class resemble the starfish in many respects. They do not furnish a satisfactory type for class use, hence no detailed description of a species is included here, but only reference to their peculiarities.

**Skeleton.** (Fig. 386). — The arms of the OPHIUROIDEA are slender and exceedingly flexible. The ambulacral groove is absent, being covered over by skeletal plates and converted into the epineural canal. Each arm is covered by four rows of plates, one aboral, one oral, and two lateral. Spines are restricted to the lateral plates. Within the arm are plates which have fused together and are known as vertebrae. The muscular system of the arm is well developed.

**Water-vascular system.** — This differs in several respects from that of the starfish. The madreporite is on the oral surface. The tube-feet have lost their locomotor function and serve as tactile organs; the ampullæ have consequently disappeared.

**Digestive system.** — The food of the brittle-stars consists of minute organisms and decaying organic matter lying on the mud of the sea bottom. It is scooped into the mouth by special tube-

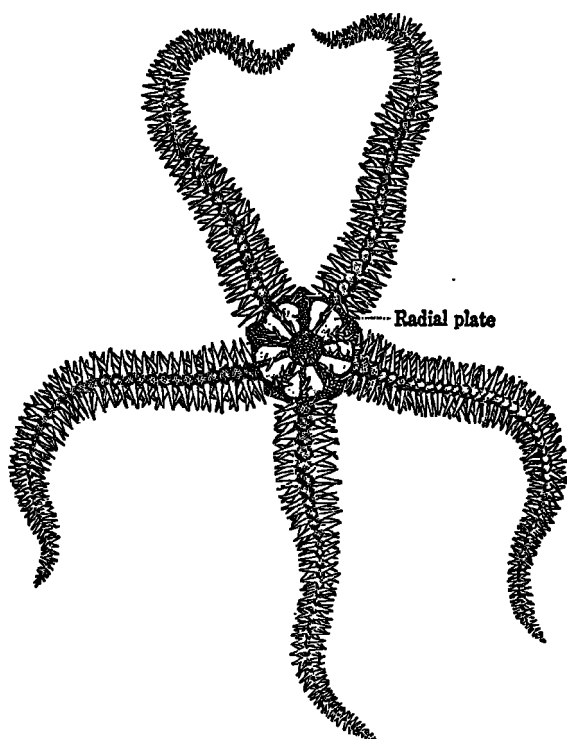


FIG. 385. — OPHIUROIDEA. *Ophiothrix fragilis*, aboral view. (After MacBride.)

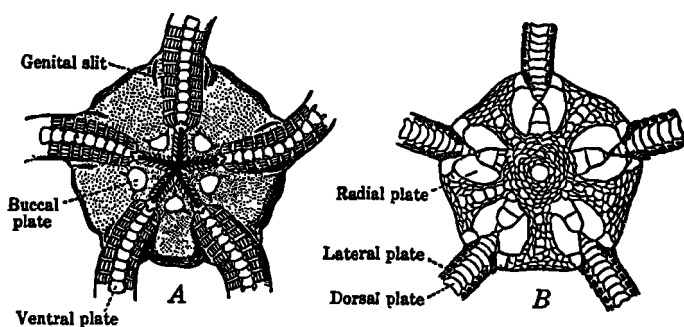


FIG. 386. — A, *Ophiura*; oral surface of disk. B, *Ophioglypha*; aboral surface of disk. (From Woods.)



feet, two pairs to each arm, called the oral tube-feet. The rows of spines which extend out over the mouth opening serve as strainers (Fig. 387). The stomach is a simple sac without ceca; it cannot be pushed out of the mouth. There is no anus.

**Reproductive system.** — The gonads discharge their products into genital bursæ which open, one on either side of the base of each arm.

**Behavior.** — The locomotion of brittle-stars is comparatively rapid. The arms are bent laterally, and enable animals belong-



FIG. 387. — *Ophiopteris papillosa*; mouth parts.  
(From Johnson and Snook.)

ing to certain species to "run," or climb, and probably swim. Apparently they cannot be taught like starfishes.

**Regeneration.** — The term brittle-star is derived from the fact that these animals break off their arms if they become injured. This autotomy often allows the individual to escape from its enemies, and is of no serious consequence, since new arms are speedily regenerated. In a number of species the aboral covering of the disk is normally cast off, probably for reproductive purposes.

**Classification.** — Two orders are recognized in the class *OPHIUROIDEA*.

**Order 1. OPHIURÆ.** — Five unbranched arms.

Family 1. OPHIODERMATIDÆ. — Disk covered with granules; oral papillæ around mouth. Ex. *Ophioderma brevispina*.

Family 2. OPHIOLEPIDIDÆ. — Disk covered with plates or scales; oral papillæ around mouth. Ex. *Ophiura sarsi*.

Family 3. AMPHIURIDÆ. — Plates on sides of arms with small,

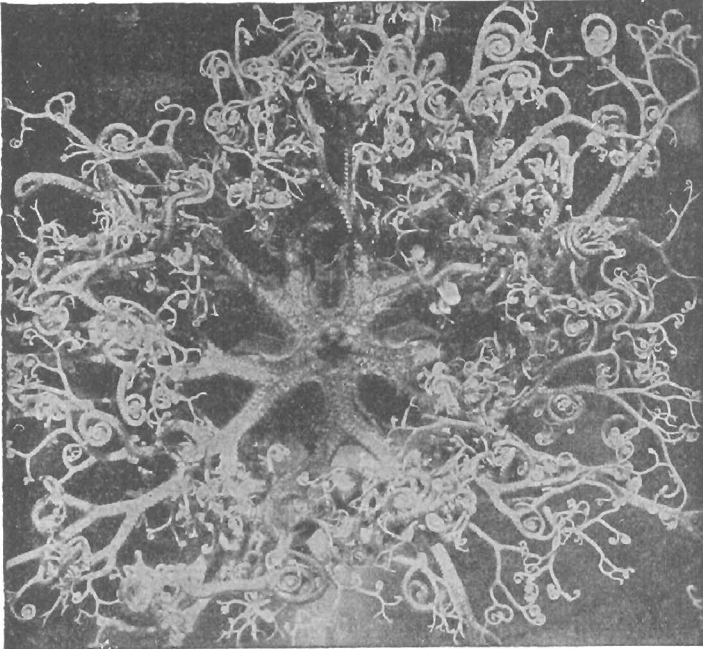


FIG. 388. — *Gorgonocephalus caryi*; photograph of a living basket star.  
(From Johnson and Snook.)

prominent solid spines; oral papillæ around mouth. Ex. *Amphipholis squamata* (a viviparous species).

Family 4. OPHIOTRICHIDÆ (Fig. 385). — Plates small on upper surface of arms; no oral papillæ; brachial spines project directly from surface. Ex. *Ophiothrix angulata*.

Order 2. EURYALÆ. — Arms may be branched.

Family 1. ASTROPHYTIDÆ (Fig. 388). — Ex. *Gorgonocephalus agassiz* (basket-fish).

### 3. CLASS III. ECHINOIDEA

#### (1) ARBACIA — A SEA-URCHIN

A sea-urchin (Fig. 389) resembles a starfish whose aboral surface has become exceedingly reduced, being represented by a

small area, the *periproct*, and the tips of whose arms have at the same time been bent upward and united near the center of the aboral surface. Both tube-feet and spines are used in locomotion. "The spines are pressed against the substratum and keep the animal from rolling over under the pull of the tube-feet and also help to push it on."

**Skeleton.** — The skeleton of the sea-urchin is known as a shell or *test*, and is shown in detail in figure 390. The *apical system* of

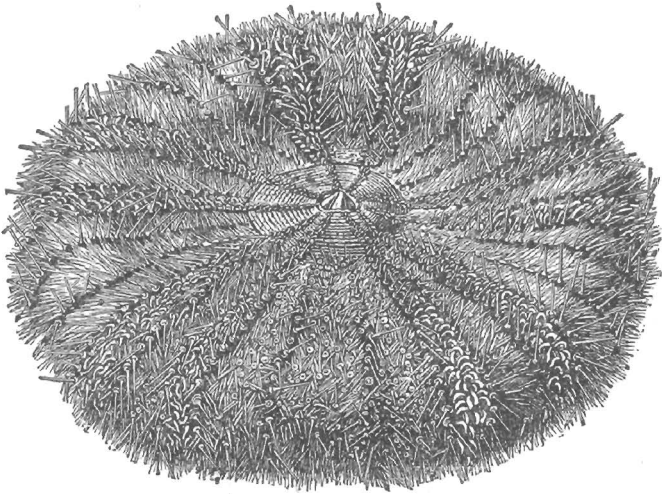


FIG. 389. — ECHINOIDEA. *Asthenosoma hystrix*; oral view of a sea-urchin. (After Thomson.)

plates contains the madreporite, four other genital plates, with genital pores, and five ocular plates, each with a mass of pigmented cells. There are five pairs of columns of *ambulacral plates*, so called because they are penetrated by tube-feet, and five pairs of columns of *interambulacral plates*. On the inside of the test around the peristome in many sea-urchins are five arches, often incomplete, called *auricles*. Most of the plates bear spines which are attached by muscles and move freely on little knob-like elevations called *tubercles*. The *pedicellariæ* are more specialized than those of the starfish; they commonly have three jaws. The mouth is provided with five white teeth; these are part of a complicated structure known as "Aristotle's Lantern."

**Digestive system** (Fig. 391). — The *food* of the sea-urchin consists of marine vegetable and animal matter which falls to the sea bottom and is ingested by means of Aristotle's lantern. That

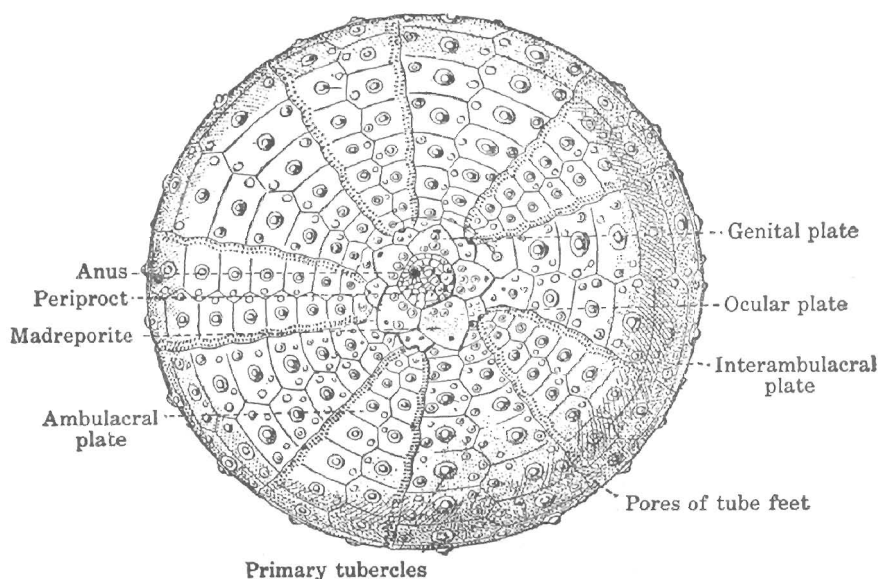


FIG. 390. -- Aboral view of the test of sea-urchin with spines removed. (From MacBride.)

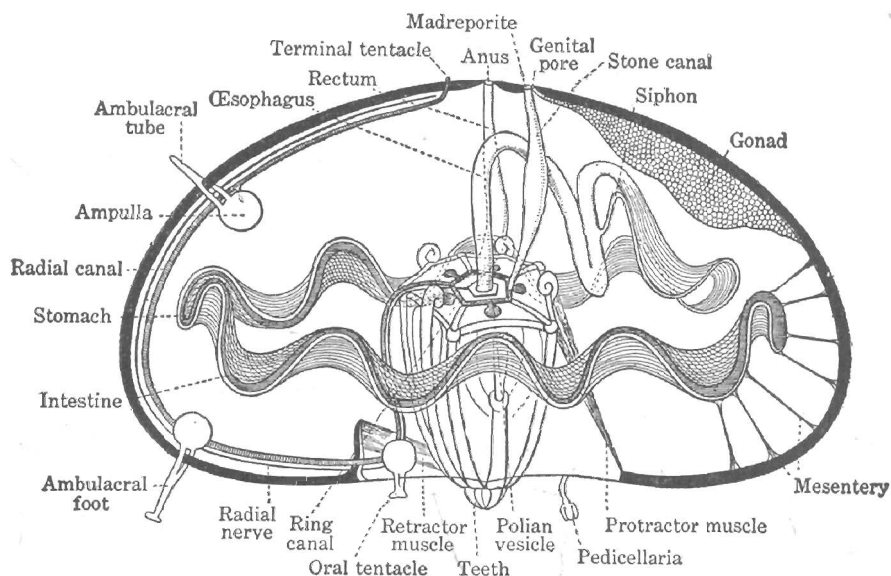


FIG. 391. -- Diagram showing the structure of a sea-urchin. (After Petrunkevitch.)

sea-urchins are capable of capturing fish may be demonstrated by placing specimens in an aquarium with a group of *Fundulus heteroclitus*. The head or tail of the fish is secured by the sea-urchin and held against the bottom or side of the aquarium by the spines and ambulacral feet while the body of the fish is gnawed away by the jaws of Aristotle's lantern. The *intestine* is very long; it takes one turn around the inside of the body and then bends upon itself and takes a turn in the opposite direction. A small tube, the *siphon*, accompanies the intestine part way opening into it at either end. The *anus* of the sea-urchin is near the center of the aboral surface.

*Aristotle's lantern* (Fig. 392) is a complicated apparatus that should command the admiration of every student of nature. The hollow axis of the lantern is formed by the *pharynx*, the body of the lantern, which has the shape of a pyramid with a pentagonal base, is composed of five complicated calcareous parts or *jaws* and as many groups of muscles. When isolated each calcareous jaw appears in the shape of a triangular pyramid. The middle portion of the tooth is enclosed between the two halves of an ossicle called the *alveolus*. The elastic free upper end of the tooth is curved over the base of the pyramid and enclosed in a pouch of the oral sinus. The horn-like processes of the alveoli serving for the attachment of the protractors are termed *epiphyses* and, though fused with the alveoli, are in reality separate ossicles. Radiating from the middle of the lantern at its base are five ossicles, the *rotulæ*, articulated to the alveoli. Below the *rotulæ* and also radial in position are five *compasses* or Y-shaped ossicles, so-called because of their two diverging ligaments. These long and thin *ligaments* arise, side by side, from the head or distal enlargement of the compass and are attached to the peristomial edge of the two adambulacral plates on each side adjoining the radius to which the ossicle belongs.

The *muscular apparatus* of the lantern is very complicated. It consists of seven sets of muscles consisting of over sixty individual muscles. Among these are the following: (1) five interpyramidal (or interalveolar) muscles; these are short; attached to the adjoining radial surfaces of the alveoli; hold the alveoli together; and close the teeth. (2) Five pairs of protractors are attached to the epiphysis and the peristomial edge of the test and run to the inside of, and parallel to the compass ligaments. (3) Five pairs of retractors are attached to the external surface of the alveoli near

the teeth and to the auricles. (4) Five muscles bind together the compasses and form the diaphragm surrounding the œsophagus. All lantern muscles are composed of smooth fibers. The entire lantern with its muscles is enclosed in the *oral sinus* formed by

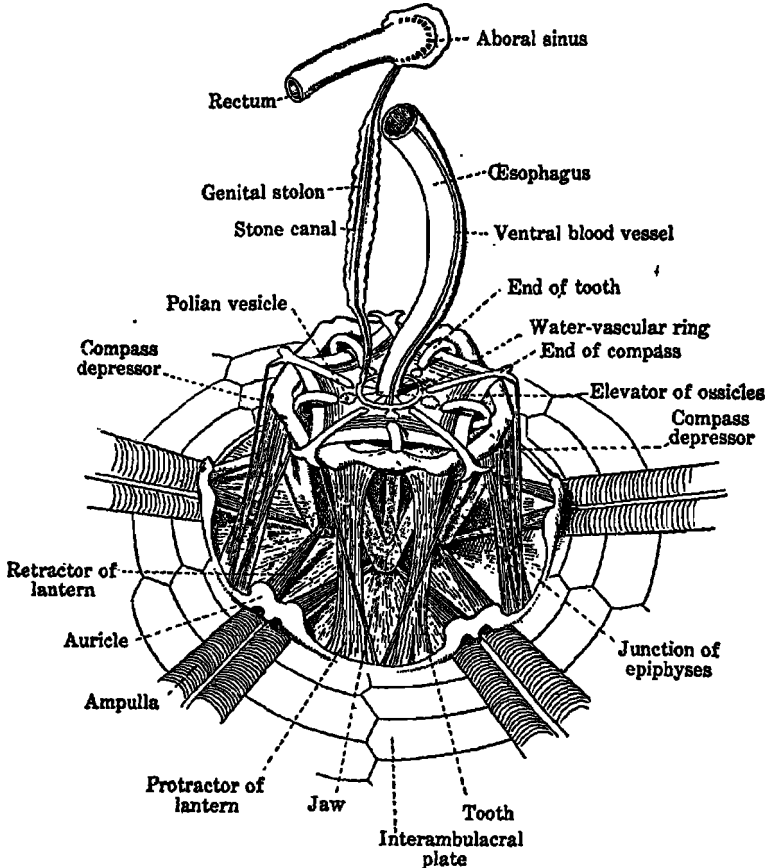


FIG. 392. — Diagram showing the structure of Aristotle's lantern in a sea-urchin. (From MacBride.)

a part of the peritoneum called the *peripharyngeal membrane*. (Petrunkévitch.)

**Water-vascular system (Fig. 391).** — One of the genital plates serves also as a *madreporite*. From the madreporite a *stone-canal* leads orally to a *circular canal* surrounding the œsophagus aboral to the lantern. From the circular canal arise five *radial canals*

and five sponge-like bodies called *Tiedemann's bodies* or *Polian vesicles*. Each radial canal leads orally and outward under the radial plates and ends in a terminal tentacle. *Transverse canals* leading to the *ambulacral feet* and *ampullæ* are given off by the

radial canals. Two pores for each ambulacral foot are present in the ambulacral plates.

#### Respiratory system.

— A large part of the respiration takes place in most echinoids through ten *branched pouches* situated on the area surrounding the mouth, one pair in each angle between the ambulacral plates. The tube-feet also are respiratory in function.

#### Locomotor organs.

— The locomotor organs of an echinoid, the sand dollar (*Echinarrachnius parma*), has recently been studied in detail. (Parker and Van Alstyne.) "The integumentary *cilia* in *Echinarrachnius* cover the tips of the short spines and the sides of the

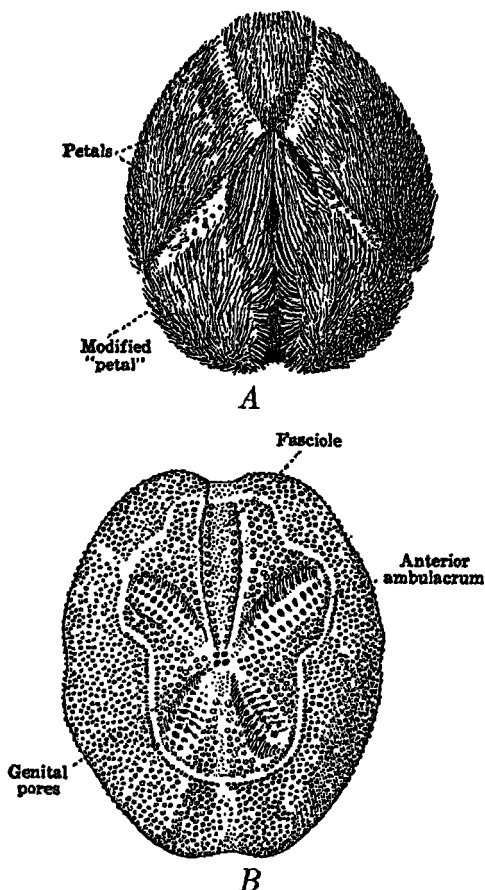


FIG. 393. — A, A heart urchin, *Echinocardium cordatum*. B, Test of a heart urchin, *Schizaster*. (A, from MacBride; B, after Agassiz.)

long ones. On the oral surface they beat radially; on the aboral they beat from anterior to posterior. They play no essential part in the locomotion of the animal, but are probably concerned with feeding, with cleaning the outer surface, and with the respiratory currents.

"The *ambulacral feet* form five complicated radial bands on the oral and the aboral sides of the test and a complete marginal fringe. Their tips are deep pink and provided with suckers. They are significant in locomotion to only a limited extent in that on the anterior edge of the test they pile up the sand on the aboral surface.

"*Spines* cover the oral and aboral surfaces. They are of two types, long and short. They are best developed over the anterior portion of the oral surface where their distribution exhibits bilateral symmetry in relation to the axis of locomotion. In this region waves of coördinated spine movement pass from the anterior edge of the test posteriorly. In these waves each spine makes a vigorous posterior thrust in a vertical plane and an unimpeded recovery in a plane more nearly lateral. Forward locomotion, burrowing, and righting are types of motion dependent primarily on these spine movements."

## (2) OTHER ECHINOIDEA

The ECHINOIDEA are subglobular or disk-shaped and without arms or free rays. The calcareous plates of the skeleton or test are closely fitted together and are usually arranged into five pairs of ambulacral rows and five pairs of interambulacral rows. The surface of the test bears tubercles with which movable spines articulate; these spines are often very long and their tips are in some species poisonous. The pedicellariæ are stalked and usually possess three jaws. Three orders are recognized.

**Order 1. ENDOCYCLICA.** — Mouth central; anus within apical area.

Family 1. ARBACIIDÆ. — Body subglobular; spines large and solid; aboral tube-feet without suckers. Ex. *Arbacia punctulata*.

Family 2. ECHINIDÆ. — Body subglobular; spines solid; periproct with many plates; ambulacral plates with three pairs of pores. Ex. *Tripneustes esculentus*.

Family 3. STRONGYLOCENTROTIDÆ. — Body subglobular; ambulacral plates with four to eleven pairs of pores. Ex. *Strongylocentrotus dröbachiensis*.

**Order 2. CLYPEASTROIDA.** — Mouth central; anus outside apical area; body usually flattened.

Family 1. CLYPEASTRIDÆ. — Body bilaterally symmetrical; shell thick; spines short. Ex. *Clypeaster subdepressus*.



Family 2. SCUTELLIDÆ. — Body flat; spines very small. Ex. *Echinarachnius parma* (sand dollar, Fig. 394).

Order 3. SPATANGOIDA. — Body cushion-shaped or heart-

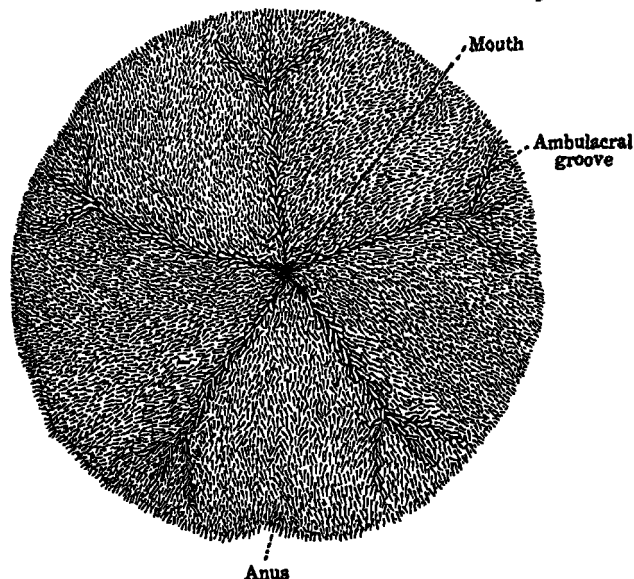


FIG. 394. — A "sand dollar," *Echinarachnius parma*, oral view. (From MacBride.)

shaped; anus, and sometimes mouth, eccentric; no Aristotle's lantern.

Family 1. SPATANGIDÆ (Fig. 393, A). — Heart-shaped. Ex. *Spatangus*.

#### 4. CLASS IV. HOLOTHURIOIDEA

##### (1) THYONE — A SEA-CUCUMBER

To this class belong the sea-cucumbers (Plate VIII, Figs. 395, 396). Their most striking external features are the *muscular body wall* almost devoid of large skeletal plates, the *branching tentacles* surrounding the mouth, and the lateral position when at rest or moving about on the sea bottom. The tube-feet, when present, are organs of locomotion. They pull the animal along on its ventral, flattened surface. Waves of muscular contraction which travel from one end of the body to the other are important in locomotion, and the tentacles may also assist.

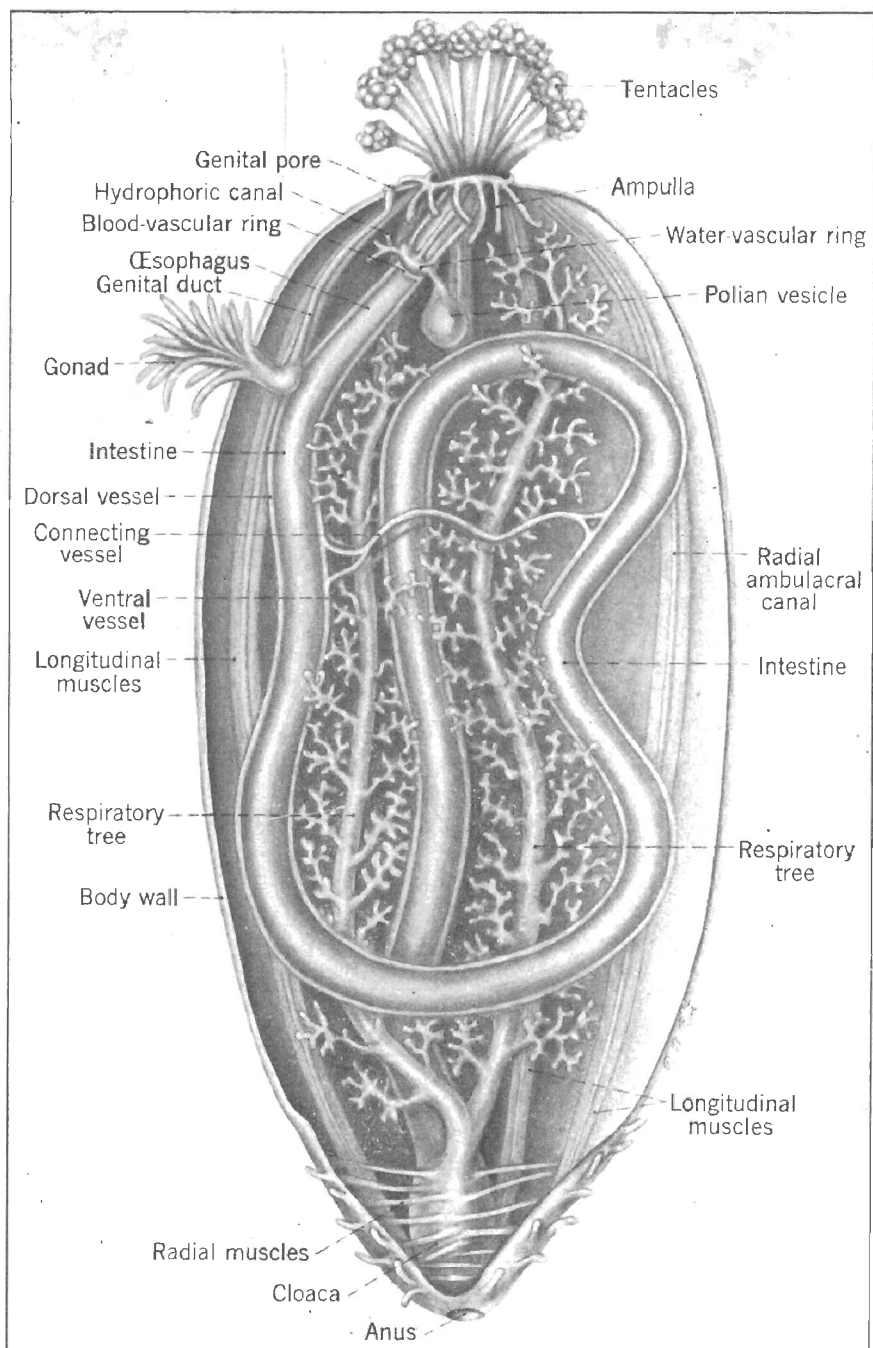


PLATE VIII. Longitudinal section of a Sea-Cucumber showing internal organs.  
(Drawn by Barbara Bradley Root.)

**Body wall.** — Instead of an articulated calcareous skeleton, the body wall is soft and *muscular* with irregular plates embedded in the dermal layer. Beneath the epidermis and dermis is a thick layer of circular muscles overlying five longitudinal muscles, each

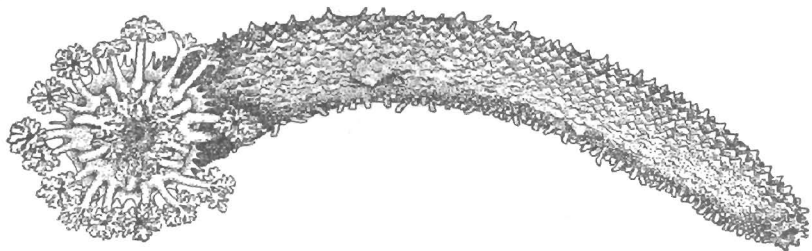


FIG. 395. — HOLOTHURIOIDEA. *Stichopus californicus*, a sea-cucumber. (From Johnson and Snook.)

of which consists of two bundles. Five retractor muscles are connected with the pharynx and a number of muscles extend from the body wall to the *cloaca* which they are able to dilate. The innermost layer of the body wall is a *ciliated peritoneal epithelium*.

**Digestive system.** — The alimentary canal consists of a cylindrical *pharynx*, a short *oesophagus*, a small muscular *stomach*, and a



FIG. 396. — *Cucumaria*; a sea-cucumber carrying its young. (After Thomson.)

long looped *intestine* the posterior end of which is a muscular enlargement called the *cloaca*. The *food* of most sea-cucumbers consists of organic particles extracted from the sand or mud which is taken into the alimentary canal. Some species are said to stretch out their seaweed-like tentacles on which many small organisms

come to rest. "When one tentacle has got a sufficient freight it is bent round and pushed into the mouth, which is closed on it. It is then forcibly drawn out through the closed lips so that all the living cargo is swept off." (Shipley and MacBride.)

**Water-vascular system.** — This is homologous to those of the other classes of echinoderms. There is a *circular canal* around the œsophagus, five *radial canals* which end blindly near the anus, and *tube-feet*. The circular canal gives off a *Polian vesicle* and one or more *stone-canals* ending in internal *madreporites*. From ten to thirty of the tube-feet surrounding the mouth are modified as *tentacles* for procuring food.

**Respiration.** — Respiration is carried on by the cloaca, *respiratory trees*, tentacles, tube-feet, and body wall. The cloaca and respiratory trees also function as excretory organs. Water flows into the cloaca through the anus and passes into two long branching tubes, the respiratory trees; here part of it probably finds its way through the walls into the body cavity.

**Behavior.** — The common sea-cucumbers, *Thyone briareus*, are sensitive to contact with solid objects, and many of them burrow in the sand or mud. They are extremely sensitive to a decrease in the light intensity and will contract the body if an object passes between them and the source of light. They are also negative to light since they move away from the source. The following has been written concerning this species: "Passing most of its life buried in the mud, *Thyone* probably does not often fall a prey to large enemies, but it is protected from them by the withdrawing reaction, by its locomotion away from the light, and by its habit of pulling eel grass and other débris over the body." (Pearse.)

**Autotomy and regeneration.** — Sea-cucumbers possess remarkable powers of autotomy and regeneration. When one is irritated it contracts the muscles of the body wall, and "since the fluid in the body cavity is practically incompressible, the effect is to set up a tremendous pressure. As a result of this, the wall of the intestine near the anus tears, and a portion or the whole of the intestine is pushed out. The gill trees are the first to go, and in some species the lower branches of these are covered with a substance which swells up in sea-water into a mass of tough white threads in which the enemies of the animal are entangled. A lobster has been rendered perfectly helpless as a consequence of rashly interfering

with a sea-cucumber. These special branches are termed Cuvierian organs.

"A Holothurioid is only temporarily inconvenienced by the loss of its internal organs. After a period of quiescence it is again furnished with the intestine and its appendages. Some species, which are able to pull in the mouth end of the body with their tentacles, when strongly irritated snap off even this, and yet are able to repair the loss." (Shipley and MacBride.)

Autotomy can be induced in *Thyone briareus* in the following manner. When an animal is placed in seven N ammonium hydroxide in the proportion of one part ammonia to 800 parts of sea-water, "there is usually a brief period of muscle relaxation and an expulsion from the cloaca of the water which filled the respiratory trees. Within 15 seconds the longitudinal and circular body muscles contract strongly, reducing the animal to minimum size. A few seconds of such contraction is followed by a gradual elongation of the anterior end of the body into which lantern, stomach, intestines, and the fluid content of the body cavity are forced. As the pressure increases, the body wall about  $\frac{1}{4}$  of an inch behind the tentacle ring becomes greatly distended. There are no strong circular muscles in this region. The body wall tissue in the distended region thins out and soon bursts allowing the body fluid to gush out carrying along with it part of the viscera. At this point in the procedure the *Thyone* is transferred to fresh sea-water. Most of the viscera are tangled around the lantern, which is partly covered over with the small portion of the body wall anterior to the break. The strong circular muscles just posterior to the break contract so as to close tightly the body cavity at the anterior end. The whole procedure to this point occupies about 30 seconds. The original break in the tissue becomes gradually more extensive until within several hours the eviscerated parts are free from the body." Of 150 *Thyone* eviscerated by this method 5 died and the other 145 lived and regenerated the lost parts. (Kille.)

## (2) OTHER HOLOTHURIOIDEA

Sea-cucumbers are elongate cylindrical animals that lie on one flattened side with the mouth at the anterior end and the anus at the posterior end. The muscular body wall contains only small calcareous particles and its external surface is free from cilia, spines, and pedicellariæ. There are ten branched oral tentacles

around the mouth, and tube feet and ambulacral tentacles may be present on other parts of the body. Among the South Pacific Islands and on the coasts of Queensland and in southern China,

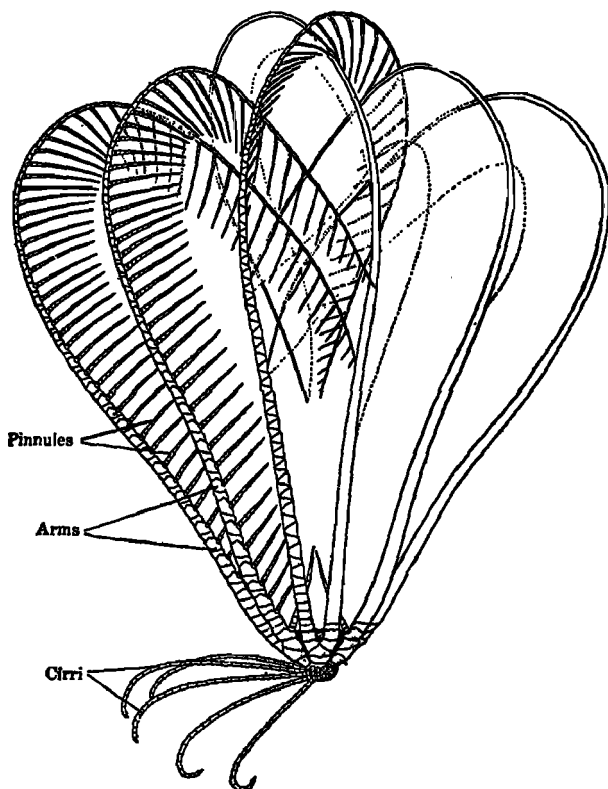


FIG. 397. — CRINOIDEA. A feather-star, *Antedon adriatica*. The pinnules on three of the arms are omitted. (After Clark.)

dried holothurians are known as “bêche-de-mer” or “trepang” and are used for food. Two orders are recognized.

Order 1. PEDATA. — With tube-feet.

Family 1. HOLOTHURIDÆ. — With usually 20 oral tentacles. Ex. *Holothuria floridana*.

Family 2. CUCUMERIIDÆ (Fig. 396). — With 10 to 20 oral tentacles. Ex. *Cucumaria frondosa*, *Thyone briareus*.

Family 3. MOLPADIIDÆ. — With usually 15 oral tentacles. Ex. *Caudina arenata*.

**Order 2. APODA.** — Without tube-feet.

**Family 1. SYNAPTIDÆ.** — *Leptosynapta inhærens*, *Chiridota lævis*.

## 5. CLASS V. CRINOIDEA

The crinoids are called sea-lilies or feather-stars (Figs. 397, 400). They are attached by the aboral apex of the body throughout life or during the early stages of their development with the oral surface above. Their arms are usually branched and bear pinnules (Fig. 398). The tube-feet are like tentacles and without ampullæ. No madreporite, spines, nor pedicellariæ are present.

There are about six hundred living representatives of this class belonging to about 150 genera and about 30 families; fossil remains are very abundant in limestone formations. Most of the living crinoids are found at moderate

depths, a few are deep-sea forms, and some inhabit shallow water. They are abundant both as individuals and as species where satisfactory living conditions exist. Crinoids are often attached by a jointed stalk. Some species break off from the stalk when they become mature, and swim about by means of muscular contractions of the arms.

The arms of crinoids are usually five in number. The apparently

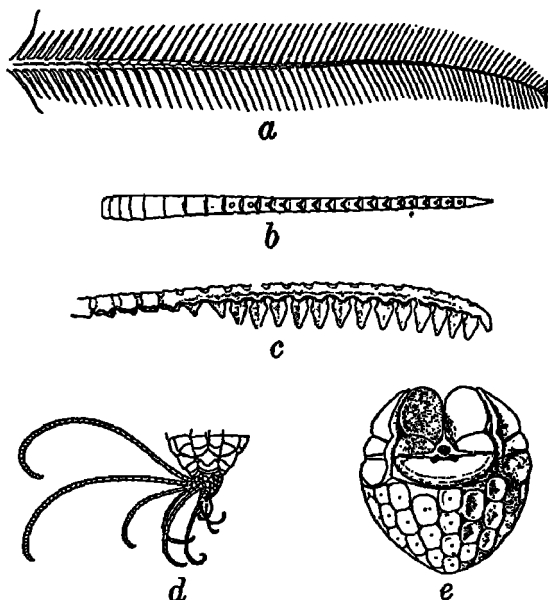


FIG. 398. — CRINOIDEA. Details of structure of several species. a, *Comatula pectinata*, grooved anterior arm. b, *Capillaster multiradiata*, cirrus with dorsal spines. c, *Leptonemaster venustus*, terminal cone on oral pinnule. d, *Nanometra bowersi*, large and small cirri. e, *Pentametrocrinus japonicus*, centrodorsal and articular faces of the radials. This is the only portion of the body that remains of most fossil feather-stars. (After Clark.)

greater number is due to branching near the base (Fig. 397). The branches may be equal, or one large and the other small; in the latter case the smaller branch is called a pinnule.

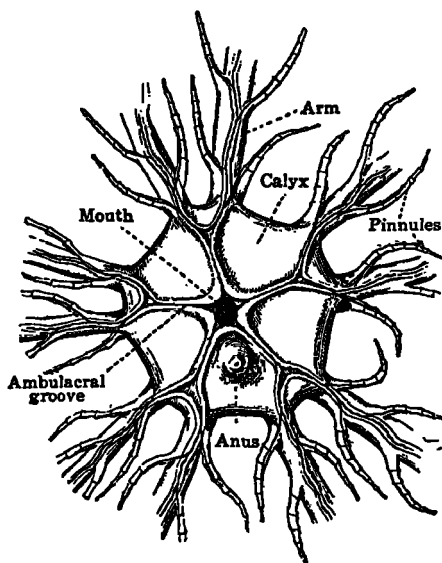


FIG. 399. — Oral view of *Antedon*.  
(From MacBride.)

**Classification.**— Living crinoids are included in two orders, the INADUNATA and the ARTICULATA. Three of the more important families are as follows.

**Family 1. PENTACRINIDÆ.**— Stalk long, with long cirri; root absent; disk small; arms divided dichotomously up to ten times; pinnules small. Ex. *Isocrinus asterias* (West Indies).

**Family 2. ANTEDONIDÆ** (Fig. 397).— Stalk present only in young; cirri at stalk base in adult; arms long,

five to twenty in number; pinnules present; over 100 species; cosmopolitan. Ex. *Antedon tenella* (Atlantic coast).

**Family 3. COMASTERIDÆ.**— Stalk present only in young; cirri few or absent at stalk base in adult; mouth eccentric; many species in tropical seas. Ex. *Neocomatella alata* (West Indies).

## 6. FOSSIL ECHINODERMS

Every class of echinoderms with living representatives includes also fossil species except the HOLOTHURIOIDEA of which only isolated ossicles have been found. The following five groups are known from fossil remains only.

**1. MACHÆRIDIA.**— The skeleton in this group consists of two or four rows of plates that resemble those of echinoderms. The animals were elongate, probably bilaterally symmetrical, flexible, and possibly attached. Ex. *Machæridian lepidocelus*.

**2. CARPOIDEA.**— In these there is good evidence of a stem for attachment. Symmetry is bilateral and the animal probably lay



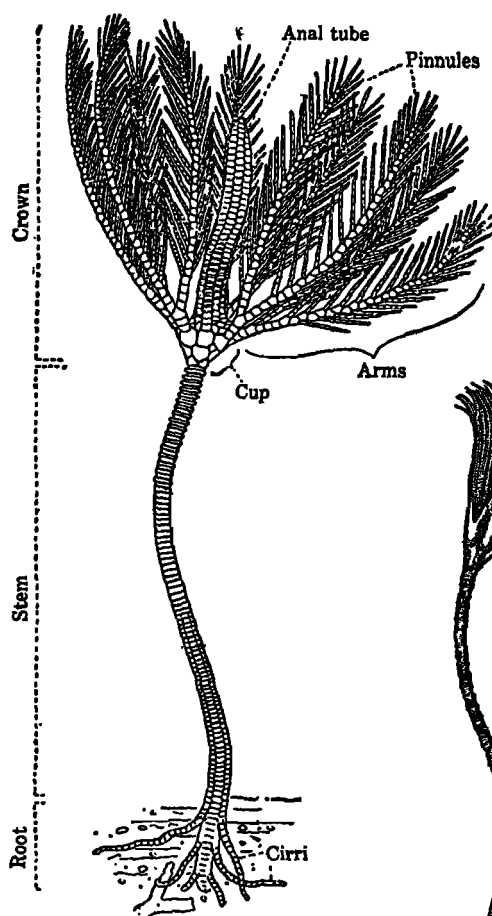


FIG. 400. — *Botryocrinus decadactylus*; a fossil erinoid. (Brit. Mus.)

taken in and genital products expelled from the opposite end. Slender, jointed appendages, the brachioles, usually surrounded the distal end. Ex. *Chirocrinus*.

4. BLASTOIDEA. — The main skeleton in these consists of thirteen plates arranged in three circlets of radials, orals, and basals. The body was attached by a jointed stem, sometimes with roots. Many brachioles are present. Ex. *Orophocrinus fusiformis* (Fig. 401, A).

flat on the bottom. No genital pore nor water pore appear to have been present. Ex. *Dendrocystis barrandei*.

3. CYSTOIDEA (Fig. 401, B). — Here radial symmetry has developed. The body was attached by a stem and food and water were

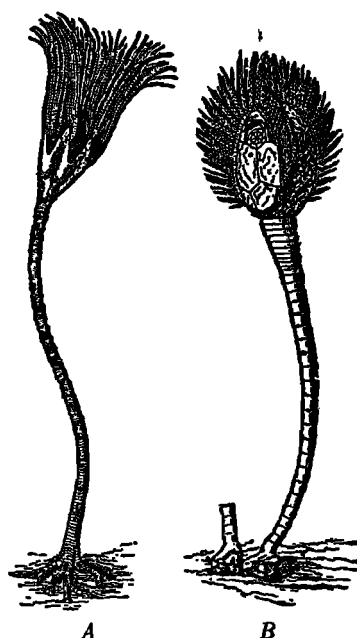


FIG. 401. — Fossil echinoderms. A, BLASTOIDEA. *Orophocrinus fusiformis*. B, CYSTOIDEA. *Lepidocrinus quadrifasciatus*. (Brit. Mus.)

5. **EDRIOASTEROIDEA.** — Here the skeleton forms a radially symmetrical circular test of many irregular plates which was attached directly to the sea bottom. Apparently a well-developed water-vascular system was present including tube-feet and ampullæ. Brachioles are absent. Ex. *Edrioaster*.

## 7. ECHINODERMS IN GENERAL

**Anatomy.** — The echinoderms are unique in the possession of radial symmetry in the adult stage, which is evidently secondary since the larvæ are bilaterally symmetrical. The number of radii is usually five.

**Body wall.** — The epidermis of echinoderms is usually ciliated and contains gland cells and sense cells. The ossicles in the body wall may be few, small, and widely scattered, or large, numerous, and united more or less firmly into a definite skeleton. Certain of the ossicles usually form spines. Pedicellariæ are often present.

**Cœlom.** — The cœlom is complex, consisting of a number of spaces including a perivisceral cavity, a perihæmal system, an aboral sinus system, a water-vascular system, a madreporic vesicle, and an axial sinus.

**Systems of organs.** — The *alimentary canal* may be axial or coiled and may possess diverticulæ. *Respiration* is accomplished in many by the tube-feet or by a respiratory tree. The tube-feet have various other functions, notably locomotion, but probably originated as sensory or food-collecting organs. No *nephridia* are present, excretory matter being taken up by amoeboid wandering cells that pass through the epithelium. No very definite *circulatory system* exists. There are strands of peculiar lacunar tissue but probably no regular circulation but rather a gradual diffusion takes place in them. The *nervous system* is primitive in type, consisting of nerve rings, radial nerves, and nerves to the tube-feet, spines, etc. *Sense organs* are not well developed. The general surface of the body is sensitive to touch and the tube-feet and terminal tentacles at the end of each radial vessel are especially sensitive to tactile stimuli. At the base of each terminal tentacle in the **ASTEROIDEA** is an eye spot. Certain holothurians possess statocysts. The sexes are usually separate. The *reproductive organs* are simple and the ova and spermatozoa are shed directly to the exterior without the aid of accessory glands, penis, seminal vesicle, and seminal receptacle.

**Development of echinoderms.** — In most of the echinoderms, the eggs pass through a ciliated blastula stage (Fig. 402), a gastrula stage, and a larval stage, which, in the course of from two weeks to two months, metamorphoses into an adult. The larvæ (Fig. 403, A) of the four principal classes of echinoderms resemble one another, but are nevertheless quite distinct. They are bilaterally symmetrical, and swim about by means of a ciliated band which may be complicated by a number of arm-like processes. The

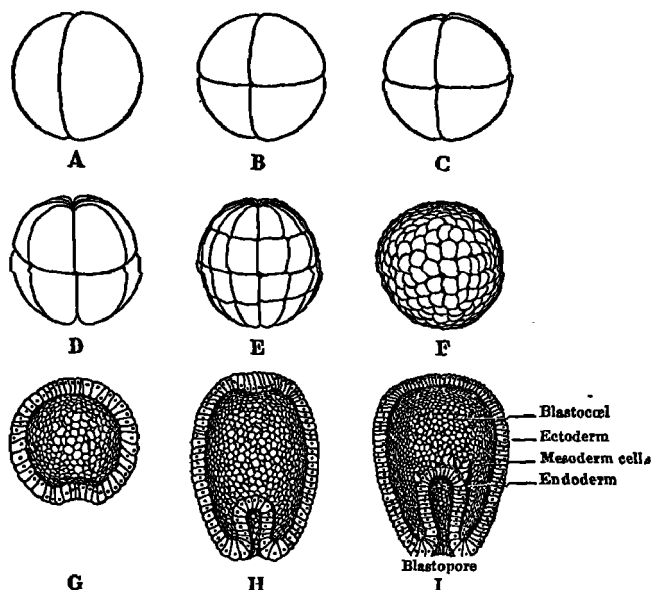


FIG. 402. — Early stages in the development of the egg of a sea-urchin. (From Woodruff.)

alimentary canal consists of a mouth, œsophagus, stomach, intestine, and anus. From the digestive tract two coelomic sacs are budded off; these develop into the body cavity, water-vascular system, and other coelomic cavities of the adult.

The larvæ of the different classes have been given names as follows: those of the ASTEROIDEA are called *Bipinnaria* (Fig. 403, C); OPHIUROIDEA, *Ophiopluteus* (D); ECHINOIDEA, *Echinopluteus*; and HOLOTHURIOIDEA, *Auricularia* (B). The adults which develop from these larvæ are, as we have seen, radially symmetrical, although many of them, notably the HOLOTHURIOIDEA, are more or less bilateral in structure. The bilateral condi-

tion of the larvæ indicates that the ancestors of the echinoderms were either bilaterally symmetrical or that the larvæ have become adapted to an active life in the water.

**Artificial parthenogenesis.**—The eggs of echinoderms pass through a total and equal cleavage, and are easily fertilized and reared to the larval stage in the laboratory. For these reasons

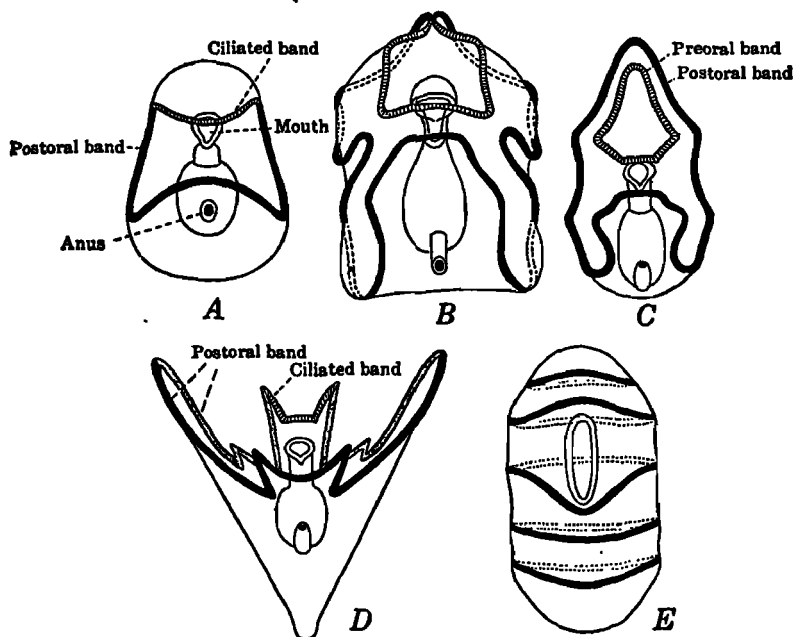


FIG. 403. — Diagrams of larval echinoderms. A, Early larval stage; B, *Auricularia*; C, *Bipinnaria*; D, *Pluteus*; E, Crinoid larva. (From Borradaile and Potts.)

they have become classical material for embryological studies and for experimental purposes.

One of the most interesting phenomena discovered by means of experiments with echinoderm eggs is the development of a larva from an unfertilized egg when subjected to certain environmental conditions. This phenomenon is known as artificial parthenogenesis. The eggs of other animals, for example, annelids, are also capable of developing under certain conditions without fertilization, and those of some species, like plant lice and rotifers are normally parthenogenetic, but echinoderm eggs have been used for experimental purposes more frequently than any others.

Loeb reared normal larvæ from unfertilized eggs of echinoderms by immersing them in solutions such as choride of sodium, potassium bromide, cane-sugar, etc. He considered the increased osmotic pressure the cause of development, and thought it probable that in ordinary fertilization the spermatozoon brings a solution with a high osmotic pressure into the egg thereby causing the withdrawal of water. Sea-water concentrated to 70 per cent of its volume has a similar result. A lowering of the temperature of sea-water to the freezing-point causes eggs of *Asterias* and *Arbacia* to develop; when combined with a chemical reagent, a higher per cent of blastulæ results. Eggs exposed to a higher temperature (35° to 38° C.) during the early maturation period develop parthenogenetically, and even mechanical agitation may have a similar effect. Normal mitotic figures appear during the cleavage of these eggs. None of the larvæ thus produced was reared to the adult stage.

The ease with which echinoderm eggs can be handled has led to some experiments that have an important bearing upon heredity. Of these may be mentioned the fertilization of the eggs of one species with the spermatozoa of another species, and the fertilization of enucleated fragments of sea-urchin's eggs with spermatozoa of another species.

**Interrelations and phylogeny of the Echinoderms.** — Echinoderms and coelenterates, because of their radial symmetry, were at one time placed together in a group called **RADIATA**. The anatomy of the adult and the structure of the larvæ, however, show that these phyla really occupy widely separated positions in the animal kingdom. The adult echinoderms cannot be compared with any other group of animals, and we must look to the larvæ for signs of relationship. The bilateral larva is either a modification for a free-swimming life or an indication of the condition of its ancestors. The latter view is accepted by most zoologists. The ancestors of echinoderms were doubtless bilateral, worm-like animals which became fixed and were then modified into radially symmetrical adults.

It is interesting to compare the development of echinoderms with that of certain primitive chordates such as *Balanoglossus*. In both, the eggs pass through the indeterminate type of cleavage; the mesoderm arises from the multiplication of cells around the lip of the blastopore; the anus evolves directly from the blasto-

pore; the mouth is formed near the anterior end of the archenteron; the coelom develops from pairs of diverticulæ of the archenteron; and the larvæ of certain echinoderms are remarkably similar to the *Tornaria* larva of *Balanoglossus*. Because of these similarities the echinoderms and chordates appear to be closely related and to have had common ancestors. For this reason these groups are sometimes placed near each other on the phylogenetic tree.

**History of our knowledge of the Echinodermata.** — The name of this phylum was introduced by Klein in 1734 as an appropriate appellation for sea-urchins. For many years the echinoderms and coelenterates were included as a class among the RADIATA, largely because of the radial symmetry of the adults. The ECHINODERMATA were first recognized as a group distinct from the RADIATA by Leuckart in 1847.

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